ECOLOGY

Vol. 40 OCTOBER, 1959 No. 4

PHYSIOCHEMICAL ENVIRONMENT OF *AUSTRALORBIS GLABRATUS*, THE SNAIL INTERMEDIATE HOST OF *SCHISTOSOMA MANSONI* IN PUERTO RICO[1]

David Pimentel[2] and Paul C. White, Jr.[3]

In previous studies dealing wtih the ecology of *Australorbis glabratus,* the snail intermediate host of *Schistosoma mansoni,* the life history, vagility, and geographic distribution of the snail were discussed (Pimentel 1957, Pimentel *et al.* 1957, and Pimentel and White 1957). This study was designed to provide information regarding the physical and chemical environments inhabited by *A. glabratus.* Such ecological information makes possible the typing of *A. glabratus* habitats and provides guidance for future studies concerning the epidemiology of *A. glabratus* and *S. mansoni.*

Two kinds of investigation were made. The first was a thorough quantitative study of the *A. glabratus* population relative to the physiochemical environment in one stream. The second was an intensive study of small portions of a great many types of water bodies geographically well distributed over Puerto Rico.

Methods

The effects of shade, turbidity, water velocity, stream gradient, bottom material, and water depth on the distribution of *A. glabratus* were studied along the entire length of a tributary of the Quebrada Sabana Llana. This stream flows over Cretaceous shale (Meyerhoff 1953) in a north-northeasterly direction to join the main stream at the village of San Martin. It is 8,094 ft long, and has an average width of 3.5 feet and a depth of less than one foot. The rainfall for the surrounding region averages 70 inches per year; the mean temperature is 25.8°C (Pico 1950). The microscopic animals and plants distributed along this stream have been included with the study of the species associates of *A. glabratus* and its habits (Pimentel and White 1959b).

The entire tributary was staked along its banks at 6-foot intervals. At each stake a one-square-yard area both up and down stream from the stake was sampled for *A. glabratus.* All the snails collected in each one-square-yard sample were counted, measured and returned to the stream at the collection site. These snails were taken from the stream in small screened (18 by 18 mesh per square inch) dip nets which were either 3 or 6 inches in diameter.

In the island-wide study, 421 stations well distributed over Puerto Rico were examined between March 1953 and May 1954. In addition to the physical factors assayed in the Quebrada Sabana Llana study, the following were added: water temperature, topography, stream channel, permanence of water and flushing effect. Studies of the chemical aspects of the snails' environment include measurements of electrolyte content, alkalinity and pH of water media. Not every type of analysis was made for each of the 421 stations.

The specific procedures and apparatus used in making the measurements will be covered in later sections.

Results

Shade

Shade was recorded for each square yard of stream as a percentage of total daylight time that a particular area was shaded. The distribution of *A. glabratus* in the Quebrada Sabana Llana was found to be influenced by shade (Table I). Fewer snails were present in the heavily shaded regions of the stream than in sunny areas (correlation of −0.66, significant at 5% level). Although the snails are negatively photoatactic and move away from intense light, they are found in sunny regions, probably because some unknown biotic requisite was present there. Further support of the negative correlation between snail abundance and intensity of shade was obtained in the island-wide survey. In an examination of 104 habitats which supported *A. glabratus* populations, the average percentage of shade covering these during the day was 6.8% and ranged from 0 to 80%.

---

[1] From the Communicable Disease Center, Bureau of State Services, Public Health Service, U. S. Department of Health, Education, and Welfare, Savannah, Georgia.

[2] Present address: Department of Entomology and Limnology, Cornell University, Ithaca, New York.

[3] Present address: 2405 Williams Lane No. 6, Decatur, Ga.

TABLE I. The percentage of *A. glabratus* population in the Quebrada Sabana Llana existing in regions with various amounts of shade and the percentage stream area shaded by different degrees

Percent Shade	Percentage of Snail Population	Percentage of Stream Included
0	15.4	17.2
10	25.7	10.9
20	11.9	14.4
30	22.0	15.5
40	11.6	10.4
50	4.8	7.3
60	2.3	5.2
70	2.2	5.4
80	2.1	1.1
90	1.9	12.8
100	0.0	0.0

Turbidity

Turbidity measurements were based on a comparison of field samples with standards of a known clay suspension. *A. glabratus* was able to exist in water of high turbidity. At the beginning of the study, the turbidity of the Quebrada Sabana Llana averaged less than 5 ppm, but, after the rainy season began, the turbidity of the lower 3,000 feet increased to from 100 to 1,000 ppm. It remained high for the following 2 months, because a large amount of clay and silt was washed into the stream from a sandpit located near the center portion of the stream. The snail population was unaffected. Data obtained in the island-wide investigation substantiated this; turbidity measured at 92 habitats containing the snail averaged 9.3 ppm and ranged from 0 to 1,000 ppm.

Water Velocity

The recorded velocity for each running yard represents measurements taken at about two-thirds depth point in midstream. Stream velocities greater than 0.17 feet per second were measured with a pygmy current meter and lower velocities by the use of floats. Stream velocity is directly related to stream gradient, and under field conditions it is nearly impossible to separate these 2 factors and their specific influence upon an animal population. However, stream gradient or the slope of the stream bed can only affect the snail *via* water velocity. In the present evaluation of the factor of water velocity, an analysis was conducted correlating stream velocity with snail abundance. A greater percentage of the snail population was associated with the slower water (Table II). This inverse relationship between snail density and water velocity was significant at the 2% level (correlation —0.99). When water velocities were measured at 70 island-wide stations containing the snail, results were similar. The water velocity in these habitats averaged 0.17 feet per second and ranged from 0.00 to 2.0. f.p.s.

TABLE II. Percentage of *A. glabratus* population in the Quebrada Sabana Llana existing in regions with various water velocities and the percentage stream length having different velocities

Velocity (feet per second)	Percentage of Snail Population	Percentage of Stream Length
0.00 to 0.10	78.0	69.2
0.11 to 0.50	15.4	13.6
0.51 to 1.00	7.1	14.2
1.01 to 1.50	0.5	1.8
1.51 to 2.00	0.0	1.2

Snails inhabiting fast moving streams were smaller than those in slow flowing streams. This seems logical because, although smaller snails (8 to 10 mm) have a greater ratio of surface area to weight than larger snails (15 to 27 mm), they can locate themselves closer to the substratum where velocities are lower

Stream gradient

Stream gradient is important to snail abundance only as it influences water velocity. Stream gradient measurement, however, may be correlated with snail abundance. Gradient measurements were made with a transit level. From the data presented in Table III there is suggested an inverse relationship between stream gradient and snail abundance in the Quebrada Sabana Llana (correlation —0.304; significance level is less than 10% but greater than 5%). Although statistically this trend is not significant, support of this inverse relationship is found in the results of the influence of water velocity. Thus, higher stream gradients resulted in greater velocity which in turn substantially reduced snail populations. Gradient calculations were made on a total of 20 streams and rivers, and the figure recorded represents an average of several measurements along the entire stream length. Substantially larger numbers of *A. glabratus* were found in streams where the average gradients were from 0.07 to 2.5% than in those with average gradients of 2.5% or more. Stream beds vary along their length, usually having a steep gradient at the headwaters and a low gradient near the mouth (Figure 1). The critical gradient was not determined for *A. glabratus* because, in the field, many other physical characteristics of the stream may also influence the snails' existence. An estimate of the gradient limit for *A. glabratus* for a section of stream is 6.25% (Table III).

TABLE III. Percentage of *A. glabratus* population in the Quebrada Sabana Llana existing in regions at various stream gradients and the percentage stream length having different gradients

Gradient (Percent Slope)	Percentage of Snail Population	Percentage of Stream Length
0.0 - 0.25	56.818	52.693
0.26- 0.50	0.000	0.783
0.51- 0.75	0.126	0.097
0.76- 1.00	17.458	1.762
1.01- 1.25	0.000	0.000
1.25- 1.50	0.479	0.881
1.51- 1.75	0.155	2.448
1.76- 2.00	0.761	3.036
2.01- 2.25	0.155	7.051
2.26- 2.50	0.310	4.015
2.51- 2.75	0.352	0.685
2.76- 3.00	21.647	6.268
3.01- 3.25	0.056	3.819
3.26- 3.50	0.211	4.211
3.51- 3.75	0.000	0.391
3.76- 4.00	0.169	2.742
4.01- 4.25	0.549	3.819
4.26- 4.50	0.141	0.293
4.51- 4.75	0.000	0.000
4.76- 5.00	0.028	1.762
5.01- 5.25	0.000	0.293
5.26- 5.50	0.000	0.000
5.51- 5.75	0.000	0.000
5.76- 6.00	0.197	1.567
6.01- 6.25	0.380	0.293
6.26- 6.50	0.000	0.000
6.51- 6.75	0.000	0.293
6.76- 7.00	0.000	0.293
8.25- 8.50	0.000	0.391
9.76-10.00	0.000	0.097

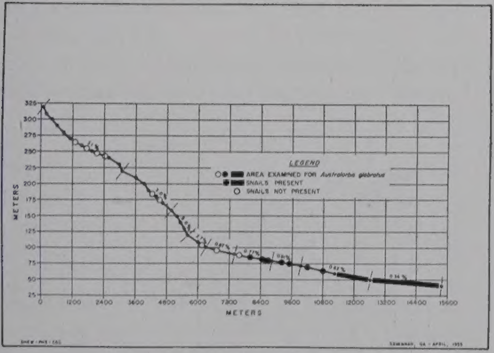


FIG. 1. A diagram of the gradient of the Rio Bairoa showing the distribution of *Australorbis glabratus* in relation to this gradient.

Bottom Material

Bottom material was measured by standard sieves and was recorded as the percentage of material passing through a certain size sieve. Although the composition of bottom material of a stream is generally a reflection of stream velocity, this measurement in itself has value in typing *A. glabratus* habitats. In the Sabana Llana 96% of the snail population was found on substratum consisting of 42% clay (passed no. 200 sieve) and 41% sand (retained on no. 60 sieve). In the island-wide survey a few snails were observed on rock bottom. Such streams, however, were usually fast flowing and subject to severe flushing action and were otherwise unsuitable for *A. glabratus* (Table IV).

TABLE IV. The results of a survey of 262 habitats having various bottom materials, 87 with and 175 without *A. glabratus*

Type of Bottom	WITH *A. glabratus*		WITHOUT *A. glabratus*	
	Number Stations	%	Number Stations	%
Muck	40	46	56	32
Sand	10	11	16	9
Gravel	24	28	37	21
Rock	13	15	66	38
Total	87	100	175	100

Water Depth

In the Sabana Llana, water depth was recorded as the average depth of stream cross-section while all island-wide measurements were recorded at the location point of the snail. The correlation between the distribution of *A. glabratus* in the Saban Llana to the depth of water was not significant (Table V). The stream cross-section statistic had definite limitations because it represented an average and did not represent the actual water

TABLE V. Percentage of *A. glabratus* population in the Quebrada Sabana Llana existing at various water depths and the percentage of stream length having different depths

Water Depth (inches)	Percentage of Snail Population	Percentage of Stream Length
0 - 3	24.0	37.6
3.1- 6	13.8	14.8
6.1- 9	12.8	11.7
9.1-12	11.1	7.7
12.1-15	12.0	9.8
15.1-18	8.6	5.0
18.1-21	1.9	2.2
21.1-24	3.6	2.7
24.1-27	1.6	1.0
27.1-30	1.2	1.4
30.1-33	2.2	1.9
33.1-36	3.0	1.1
36.1-39	2.9	0.4
39.1-42	0.1	0.6
42.1-45	0.0	0.4
45.1-48	1.2	1.7

depth over the snail population. In the island-wide survey no snails were observed in water with a depth greater than 3.5 feet.

Water Temperature

A. glabratus was encountered in 113 widely scattered water bodies which had an average temperature of 26.7°C (maximum 37°—minimum 21°). The 37°C temperature was registered in a marshy area near the mouth of the Rio Guajataca, where there were 3 inches of water over a black muck bottom which was lightly shaded by *Typha*. The high temperature was due both to the shallowness of the water and the high absorption by the black mud. The ability of the snails to exist in such water is substantiated by the laboratory studies of Brumpt (1941). He exposed *A. glabratus* to 37°C temperatures and found they could survive for only 3 or 4 days. Further experiments by Brumpt indicated that snails could survive excessive heat of day if the temperature was reduced to about 25°C at night, and that they survive for short periods at temperatures in excess of 33°C and below 10°C.

Topography

Topography influences the severity of stream flushing. Streams located in areas of steep-sloped barren hills where a large drainage area collects run-off rapidly are subject to severe stream flushing after heavy rainfall. A typical example of this was a section of the Rio de la Plata which flowed through the steep mountain valley of Comerio. At the end of a low rainfall period in April, 1953 it contained an average of 97.4 snails per square yard. Shortly after the rainy season began, snails averaged only 0.8 snails per square yard. Here the rugged topography heightened the effect of rainfall in flushing the stream and accounted for the virtual elimination of *A. glabratus* from the river.

The topography of the upper water-shed of the Quebrada Blasina was in sharp contrast to this for it had a small alluvial drainage area which allowed the rain water to run into the stream slowly. In addition, the stream in this area was supplied by many springs which provided a large and constant supply of water. Snails were prevalent throughout the year and were little affected by the heavy rains and stream flushing.

Canals, draining large flat territories, were also little affected by heavy rains, for the rain seeped slowly into these canals.

Flushing Effect

Rainfall increases water levels and stream velocities and ultimately causes flushing of the streams. Flood stage level was selected to measure the effect of a single flushing on snail population. Stream stage level gauges with continuous recording devices were constructed on each of 3 streams and on one river. For each body of water records on stage level were initiated on April 23, 1953, and maintained through June 30, 1954. Permanent stations were marked for the measurement of snail populations. In each of 4 well distributed sections along both the Quebrada Sabana Llana tributary and the Quebrada Dona Ana and in each of 7 sections of the Rio de La Plata, 5 stations were established. Five stations were located along the Quebrada San Martin. A weekly count was made of the number of *A. glabratus* found in the one-square-yard area directly in front of a stake at each station.

The flood stage level data fluctuated within relatively narrow limits. However, the weekly snail population data fluctuated markedly. These weekly variations in the snail population indices seemed to mask the effect that any one flood stage had on snail population density. Though desired, more extensive population measurements were not feasible at the time.

On May 2, 1953 about 2 inches of rain fell and the water level in the Quebrada Dona Ana rose 3.4 feet above the normal depth of 1.5 feet. The stream was flushed, causing a reduction in the snail population of 73% (significant at 5% level) (Figure 2). The effect of the subsequent flood stages on the snail population was not immediately apparent in the weekly population measurements but could be detected in the gradual decline of the population, similar to the trend shown after May 5, 1953 in Figure 2.

Rainfall data were evaluated to see if they showed a clearer association with snail abundance

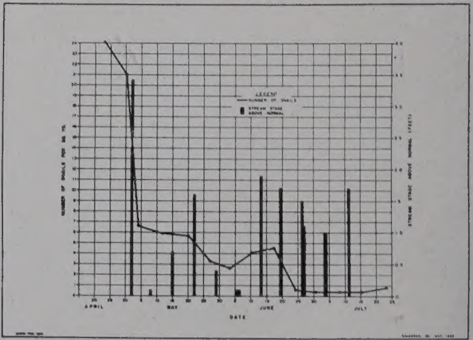


FIG. 2. The decline in the average number of *Australorbis glabratus* per square yard at 20 permanent stations in the Quebrada Dona Ana caused by flood stages.

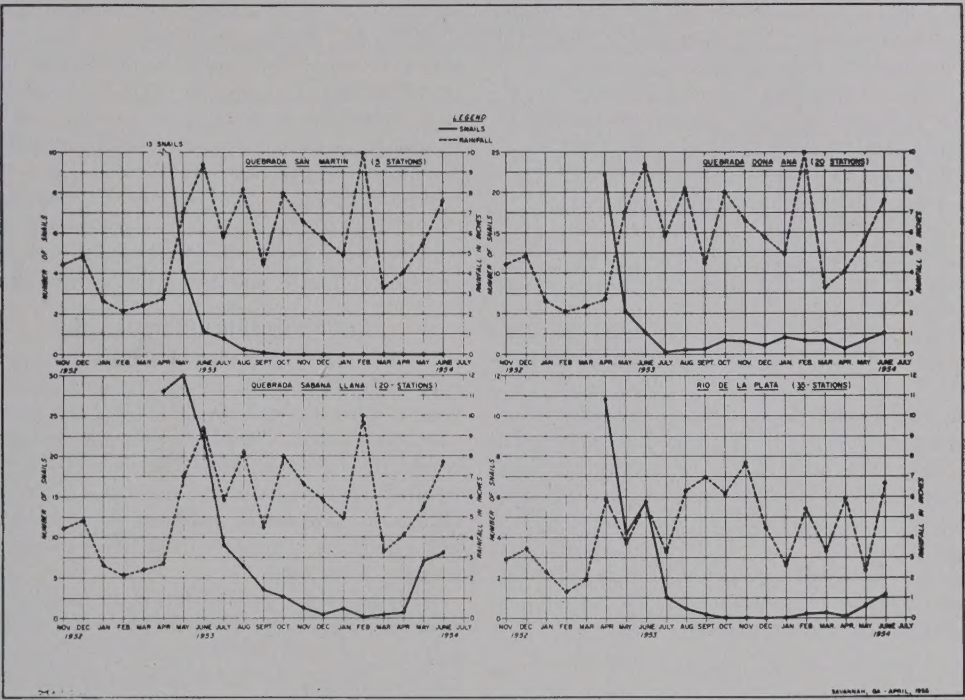


FIG. 3. The average number of snails present per square yard in various flowing waters as influenced by flushing and rainfall (number of permanent stations examined weekly on each body is written in parentheses beside name of water body).

than did flood stage level data. These data were obtained from the U.S. Weather Bureau Station closest to each test stream for several months previous to the start of the population measurements and during 15 months of the experiment. Rainfall data of this type have definite limitations because they do not indicate the irregular fall of rain over an area. Comparison of rainfall data with snail population data from the Quebrada Dona Ana, and the Quebrada Sabana Llana, the Quebrada San Martin and the Rio de La Plata is shown in Figure 3. Weather Bureau data showed that a period of abnormally low rainfall had preceded the initial population measurements. As rainfall became heavy during the latter part of April and the beginning of May 1953, the streams were observed to be flushed severely and the snail populations reduced to a low level. Based on the known reproductive potential of the species (Pimentel 1957), there seems little doubt but that the large populations observed in April had developed during the drought period which provided a certain stability to the stream environment. The snail populations remained low for the ensuing 11 months while the rainfall continued to be heavy. At the Quebrada Sabana Llana rainfall was slightly low for March and April, 1954, and increased again in May and June. In the vicinity of the Rio de La Plata the precipitation did not decrease. During May and June, 1954, the snail populations in both streams increased slightly. The dry period at the Sabana Llana, however, was not long enough to account for the increase in snail population during May and June, 1954, since the average life cycle of the snail is 3 months. These unexplained increases indicate that more than one factor controls the density of snail populations. A rapid regrowth of vegetation, as was observed in some sections of the stream, would offer the snail protection and food. This and other factors, in all probability, made it possible for the snail populations in the Sabana Llana and Rio de La Plata to increase slightly during May and June, 1954. When interpreting monthly rainfall data, the fact that a single heavy rain has greater flushing effects than the same quantity of water falling as light showers over a period of days must be considered. While the data in Figure 3 must be interpreted with the limitations noted, they do show that snail populations were much lower during a period of heavy rainfall than immediately following a dry period.

To study further the relationship of flushing to snail abundance, conditions on the Rio Bairoa were investigated. On November 6, 1953, at 5 stations located along the lower part of the river, an average of 193 snails were counted per square yard. A heavy rain (1.7 inches) fell in the vicinity on the following 2 days causing the river to rise in height from the one foot norm to a depth of 3 feet. The snail population was reduced by 98% to an average of 4 snails per square yard. A t-test comparison of samples before and after indicated the reduction of snail population was significant (1% level).

In general, any stream that reached a flood stage of more than twice its normal depth flushed severely. Observations indicated that about 75% of the loss in snail populations (10 to 90% reduction) as a result of flushing was due to stranding on banks, the other 25% were lost by being pounded against obstructions by the turbulant water or washed into the ocean. The extent to which heavy rains and high flood stage levels affect the density of snail populations is influenced directly by channel shape, topography surrounding the stream, and stream gradient.

Stream Channel

The type of stream channel affects stream velocity, influences snail distribution, and determines the amount of stranding occurring during flooding. The importance of stream velocity to the ecology of *A. glabratus* has been discussed. The lower the ratio of channel boundary to stream cross-sectional area, the greater the water velocity and there is less chance for microenvironments with low velocities. Deep-sloped banks (V-shaped), permitting water to rise rapidly during flood stage and yet confining it to the channel, have the effect of producing high water velocities. Streams so characterized were unfavorable for the snail even when they had a low gradient and were located on alluvium.

Streams with shallow, low-sloped banks, provided microenvironments of low water velocities suitable for the snail. During flood stage, the water level rose only slightly before it overflowed into the surrounding flood plain. Although water velocities were reduced as the water passed through the vegetation on the flood plain, the snails were often left stranded. The snails are not adapted to following receding water (Pimentel and White 1959b), and substantial numbers were left stranded following a stream flooding.

Permanence of Waterbody

A. glabratus was not observed inhabiting temporary bodies of water. The average generation time for the snail is about 3 months (Pimentel 1957) and so a pond would have to contain water between 3 and 6 months to allow time for a minimum of one generation. The combination of high death rate during aestivation and exposure to predation prevents snails from inhabiting any temporary waterbody (Pimentel and White 1959b). Also, *A. glabratus* is not vagile (Pimental *et al.* 1957) and, when a temporary waterbody becomes dry, the snail population cannot emigrate and locate another suitable environment.

Chemistry of the Water Medium

In only one place was *A. glabratus* found in aquatic habitats with a high percentage of sea water. This was at the margin of a brackish water zone on Vieques Island, Puerto Rico where the sea-water content ranged from 5 to 10%. It is pertinent to note here that Brumpt (1941) maintained *A. glabratus* in 20% sea water for periods up to 35 days. Probably the 20% is a near maximum for the snail.

Another factor in the environment which may affect the snail is the rapid change which may take place in the total dissolved solids content of the water. The problem is simply whether the osmoregulatory system of the snail is capable of adjusting to rapid changes. Normally, water flowing over alluvium has a high total solids content, but this is always subject to dilution from heavy rains. Based on field observations, snails appear able to survive conditions of relative rapid changes in the total solids content. The mortality occurring during heavy rainfall can usually be attributed to flushing and subsequent stranding.

When field collected snails were transferred to laboratory habitats there was a high (about 10%) death rate which seemed to be associated with the differences between the 2 habitats. An attempt was made to study the sensitivity of the snail's osmoregulatory system to change in total solids content of the habitat. A series of preliminary laboratory experiments was conducted, using snails from 3 natural habitats. The first group, originally from the Rio Bairoa, were maintained in the laboratory for 3 months before exposure to a test habitat which consisted of a sand bottom, a spring of *Najas guadalupensis,* and water composed of half from the Quebrada Dona Ana and half tap water. These snails are hereafter called laboratory snails. The electrolyte solids content of this medium, as indicated by the conductance[5]

---

[5] Conductance is defined as the reciprocal of resistance, and is expressed in reciprocal ohms, or "mhos". The micromho, or μmho, (10^{-6} mho), is used as the unit of conductance throughout this paper.

Table VI. The percentage mortality and hemorrhaging during death of *A. glabratus* from 3 different habitats exposed to 4 experimental habitats for 14 days

Water Source	Added Food	Habitat conductance µmhos	Snail Group					
			Rio Bairoa		Laboratory		Rio Grand de Loiza	
			Mortality Percent ± S.E.	Hemorrhaging Percent ± S.E.	Mortality Percent ± S.E.	Hemorrhaging Percent ± S.E.	Mortality Percent ± S.E.	Hemorrhaging Percent ± S.E.
Distilled	Rice, Apple Pumice	16.6	100 ± 0	50 ± 26	100 ± 0	15 ± 4	80 ± 0	30 ± 13
	Dog food, Dried Skim Milk	50	80 ± 41	2 ± 4	....	...	42 ± 20	0
Quebrada Dona Ana	Rice, Apple Pumice	286	35 ± 19	0	0	0	52 ± 18	5 ± 0
	Dog food, Dried Skim Milk	333	35 ± 26	2 ± 4	0	0	50 ± 13	0

of the water, was 203 µmho. The second group of snails was collected near the mouth of the Rio Bairoa where the conductance of the water was 357 µmho. The third group was collected in the upper portion of the Rio Grande de Loiza, where the conductance of the water was 149 µmho indicating water lowest in total electrolytes of the 3 habitats.

Twenty snails from each of the 3 habitats were individually exposed for 14 days to each of 4 treatments. The 4 treatments consisted of 2 types of water media and 2 diets. Distilled water (conductance 5.5 µmho) was used as one medium, and water from the Quebrada Dona Ana (conductance 286 µmho) was used as the other medium. One diet was a low mineral diet of rice and apple pumice, and the other was a high mineral diet of dog food and dried skim milk. The experiment was replicated twice. Food, especially the high mineral content diet, increased the conductance of the water (Table VI), especially in the distilled water.

In the distilled water-low mineral habitat, 100% of the Bairoa and laboratory snails died and 80% of the Loiza died. A high percentage of snails hemorrhaged in this low mineral habitat. This indicated that the osmoregulatory system of the snail was unable to prevent the entrance of an excess amount of water. Hydrolysis occurred in many cases to such an extent that the bodies of snails burst. The largest number of deaths in all 3 groups occurred between the second and seventh days of the 14-day exposure period. The Loiza snails were better able to resist the distilled water than were either the Bairoa or the laboratory group probably because these snails came from a natural habitat in which the water was already low in total electrolytes.

The conductance of the distilled water-high mineral habitat was higher than that of the distilled water-low mineral habitat and the mortalities of the 2 groups tested were correspondingly lower (Table VI). (Note: laboratory-maintained snails were not included.) The Loiza snails from the relatively dilute river water survived better than the Bairoa snails which came from water high in total electrolytes.

The conductance of the Quebrada Dona Ana water plus the low-mineral diet or the high-mineral diet were similar so the data from these groups can be evaluated together. The Loiza snails experienced the highest mortalities, Bairoa next, and the laboratory group least. Though the data are quite variable, these 2 experimental habitats seem to have been below the range of conductance values tolerated by the Loiza group of snails. The laboratory snails had been maintained in a habitat containing one-half tap water and the conductance readings of both test habitats were close to the original one.

An interesting observation made with both the laboratory colonies and field-collected snails was that all groups had a burst of egg laying when placed in their new environments. These eggs were viable.

In nature, snails are able to exist in waters which have varying amounts of electrolytes. They may be selectively bred to survive in waters with a certain quantity of electrolytes or they may become acclimated to the specific habitat in which they hatched. Support of the latter possibility is found in the results of laboratory tests in which all the progeny from a group of field-collected snails, sensitive to water of low solids, were reared in a medium relatively low in total solids and were able to survive with little or no mortality. If this difference had been genetic, a significant portion of the progeny from the sensitive snails should have died. Brumpt's (1941) observations also substantiate this theory. He found that snails could be changed from a habitat with a low concentration of solids to one containing a high concentration by progressively acclimating the snails to the new habitat.

The importance of the sensitivity of *A. glabratus* to changes in total electrolyte content of the medium in nature is not known. Based on the observation reported, this factor would appear to have little effect on the snail as it exists in its natural habitat. Rain seldom dilutes a habitat sufficiently and for a long enough period to adversely affect a snail population and drought conditions certainly should not increase the dissolved solids content rapidly enough to affect the snail population.

No significant difference was found in pH, alkalinity and conductance when water from 26 *A. glabratus* habitats was compared with that from 26 habitats devoid of snails (Table VII).

TABLE VII. Survey of 26 aquatic habitats with and 26 aquatic habitats without *A. glabratus*

Analysis	*A. glabratus* PRESENT		*A. glabratus* ABSENT	
	Ave.	Range	Ave.	Range
pH	7.64	6.5-9.0	7.84	6.6-8.9
Alkalinity CO_2 (p.p.m.)	3.2	0- 56	6.6	0- 86
$CaCO_3$ (p.p.m.)	116.5	40- 324	101.6	10- 210
Conductance µmhos	322	149-1820	251	100-1724

In the field, the only observed chemical limit in the aquatic habitat was extremely heavy pollution (raw sewage) or brackish water. Light to medium pollution increased food and such areas actually supported more snails than was usual in otherwise similar areas.

This pulmonate snail obtains oxygen from the water medium by means of gills and from the air by means of the respiratory sac. It is not strictly dependent upon the dissolved oxygen content of water.

SUMMARY

This study, designed to provide field evidence regarding the physical and chemical environment of *A. glabratus* in Puerto Rico, showed that:

1. Snail abundance was inversely related to degree of shading.
2. Turbidity did not noticeably affect the viability of the snail.
3. Snail abundance was inversely related to stream velocity.
4. Substantial evidence suggested snail abundance was inversely related with stream gradient.
5. Bottom material did not affect *A. glabratus* directly but indicated types of habitats where the snail is usually found, *i.e.* muck bottoms.
6. The snail was generally found in shallow water.
7. In environments inhabited by the snail, water temperatures averaged 26.7°C. and ranged from 21 to 37°C.
8. The snail was present in streams with alluvial watersheds but not in streams with watersheds of steep-sloped barren hills where runoff rates and flushing action were high.
9. The flushing of streams caused severe reductions in the snail populations because many snails were washed out into the flood plains and left stranded.
10. Stream channels with deep, steep-sloped banks (V-shaped) were less suited for *A. glabratus* than channels with shallow, low-sloped banks.
11. The snail did not inhabit temporary water.
12. The osmoregulatory system of the snail was not well adapted to rapid changes from one habitat of a certain total electrolyte content to another with a different level, even when the species tolerance was not exceeded.
13. Snails placed into a new aquatic environment with a marked difference in total electrolyte content usually had a burst of egg laying.
14. No differences in pH, alkalinity, and conductance were detected between habitats with and without *A. glabratus*.
15. Extremely heavy pollution was unsuited for the snail but light pollution provided abundant food for the snail. Brackish water limited the distribution of the snail.

ACKNOWLEDGMENTS

The authors are particularly indebted to Dr. Harold W. Harry, U.S. Army Tropical Research Medical Laboratory, for suggesting to them that the conductance measurement of water from a habitat was a possible means of distinguishing suitable and unsuitable *Australorbis glabratus* habitats. Dr. Harry was also generous enough to run all conductance analyses of our water samples.

The authors also thank Mr. J. W. Klock, Mr. Victor Ildefonso, Mr. Roland Cancel, and Mrs. Aida Z. deColon for their technical assistance in making many of the routine observations.

References

Brumpt, E. 1941. Observations biologiques diverses concernant *Planorbis* (*Australorbis*) *glabratus* hote intermediare de *Schistosoma mansoni*. Ann. De Parasit. Vol. **18**(1-2-3): 9-44.

Meyerhoff, H. A. 1933. The geology of Puerto Rico. Monogr. Univ. P. R., Ser. B. No. 1.

Pico, Rafael. 1950. The geographic regions of Puerto Rico. Univ. of P. R., Rio Piedras, P. R.

Pimentel, D. 1957. Life history of *Australorbis glabratus*, snail intermediate host of *Schistosoma mansoni* in Puerto Rico. Ecology **38**: 576-580.

——— **and P. C. White, Jr.** 1959b. Biological environment and habits of *Australorbis glabratus*. Ecology **40**: 541-550.

———. 1957. Geographic distribution of *Australorbis glabratus*, the snail intermediate host of *Schistosoma mansoni* in Puerto Rico. Amer. Jour. Trip. Med. Hyg. **6**: 1087-1096.

——— and **Victor Ildefonso.** 1957. Vagility of *Australorbis glabratus*, the snail intermediate host of *Schistosoma mansoni* in Puerto Rico. Amer. Jour. Trop. Med. Hyg. **6**: 576-580.

BIOLOGICAL ENVIRONMENT AND HABITS OF *AUSTRALORBIS GLABRATUS*[1]

David Pimentel[2] and Paul C. White, Jr.[3]

In other studies of the ecology of *Australorbis glabratus*, the life history, vagility, geographic distribution, and the physiochemical environment of the snail are discussed (Pimentel 1957, Pimentel *et al.* 1957, Pimentel and White 1957, 1959). The present study was designed to evaluate the association of various animals and plants with the snail and record some of its behavior characteristics. Three separate investigations were made. The first entailed a detailed study of large portions of 2 streams, the Quebrada Sabana Llana inhabited by *A. glabratus* and the Quebrada Maracuta without the snail. The second was a careful study of portions of a great many types of water bodies distributed over the island. The third included studies of various habits of the snail.

A Comparison of Two Streams

Method

During March, April, and May 1953, the animal life and vegetation were studied along the entire length of a tributary of the Quebrada Sabana Llana. This tributary, as described by Pimentel and White (1959a), was staked along its banks at 6-foot intervals and on both sides of each stake, one square yard of stream area was sampled for animal life. All the *A. glabratus* collected in each square yard sample were counted, measured for maximum diameter, and returned to the stream. The animals recorded as being associated with the snail consisted of macroscopic animals collected or observed while specifically sampling for *A. glabratus*. Since the sampling technique was specific for *A. glabratus*, the animal samples were biased accordingly.

A record was made of the macroscopic plants growing in each of the 2,698 square yard areas sampled. Plants recorded were either those observed directly or those collected on the nets while sampling for *A. glabratus*.

Using similar techniques, the fauna and flora of the Quebrada Maracuta were studied during March through May, 1954, in 5 areas each 200 feet in length and well distributed along the water course. This stream was selected because it contrasted sharply with the Sabana Llana in that it did not contain *A. glabratus* and is located in a totally different physiographic region of Puerto Rico. The Maracuta flows over old land pyroclastic rock (Myerhoff 1933) in a northerly direction and empties into the Rio Grande de Lozia. It is 7 miles long and has an average width of 6 feet and average depth of 1.5 feet. The average yearly rainfall for the region is 75 inches and the mean annual temperature is 24.5°C. (Pico 1950). The surrounding region is marked with steep-sloped mountains as compared with rolling hills near the Sabana Llana; herbaceous and woody growth is less dense than in the Sabana Llana region.

Results

In the Sabana Llana 12,592 snails were collected and measured. They averaged 10.87 mm in size, but this average is not a true picture of the population since the size distribution curve was bimodal (Figure 1). It is possible the 2 size groups (size and age are correlated, see Pimentel 1957) were the result of an environmental change which killed many small snails (less than 4 or 5 mm) shortly before the survey. Most likely, however, the groups are the result of a difference in microenvironmental requirements between the large and small snails. In the sections of the Sabana Llana where fine-leafed aquatic plants were present, the snail population consisted predominately of small snails (1 to 4 mm) (Table I). The dense growth of fine-leafed aquatic plants inhabited by the small snails probably provided protection against being washed downstream or prayed upon by other animals. The large snails (15 to 21 mm) were found in many kinds of habitats in the stream (Table I).

---

[1] From Communicable Disease Center, Public Health Service, U. S. Department of Health, Education, and Welfare, Savannah, Georgia.

[2] Present address: Department of Entomology and Limnology, Cornell University, Ithaca, N. Y.

[3] Present address: 2405 Williams Lane, No. 6, Decatur, Georgia.

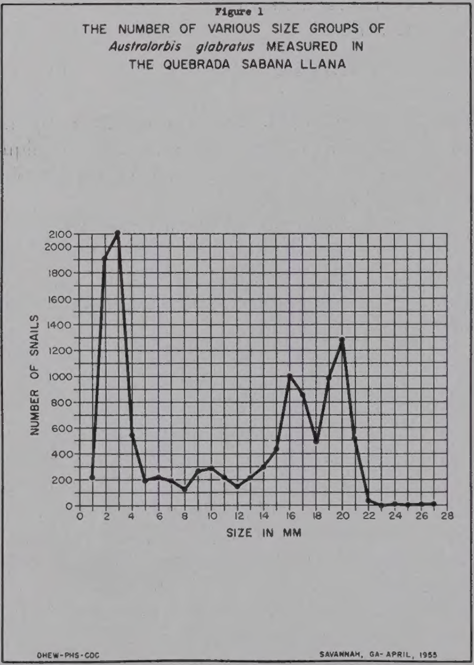


Figure 1

THE NUMBER OF VARIOUS SIZE GROUPS OF *Australorbis glabratus* MEASURED IN THE QUEBRADA SABANA LLANA

TABLE I. The percentages of small and large *A. glabratus* in the Quebrada Sabana Llana tributary in habitats without macroscopic plants and in habitats with certain type macroscopic plants

	Number Plants	Submerged and Floating Plants	Encroaching and Emergent Plants
Small snails (1 to 4 mm.).....	11	77	12
Large snails 15 to 21 mm.)....	34	32	34
Percentage stream area with habitat types indicated......	36	16	48

The majority of the large snails were present at or near sewage outlets where food was especially abundant. In addition, the number of large snails in a population tends to increase in time because they live for a longer period of time at this size.

The macroscopic vegetation consisted chiefly of 11 plant groups. Although the aquatic plants covered only 15.6% of the total surface area of the stream, 53.0% of the *A. glabratus* population was associated with the aquatic plants (Table II).

TABLE II. Percentage stream area of the Quebrada Sabana Llana tributary and the Quebrada Maracuta covered with plants[1] and the percentage of *A. glabratus* associated with each plant species on the Sabana Llana tributary

	QUEBRADA SABANA LLANA TRIBUTARY		QUEBRADA MARACUTA
Plant	Percentage Stream Area Covered	Percentage of *A. glabratus* present	Percentage Stream Area Covered
I. SUBMERGED & FLOATING.........	*15.61*	*53.0*	*8.61*
Nitella........................	9.21	39.0	0.0
Najas quadalupensis............	2.97	5.0	0.0
Compsopogon..................	1.00	4.0	6.63
Cladophora.....................	1.76	2.0	0.98
Spirogyra......................	0.67	3.0	1.00
II. ENCROACHING & EMERGENT......	*48.39*	*24.0*	*0.0*
Araceae *Caladium*..............	33.99	12.0	0.0
Commelinaceae *Commelina*......	8.49	6.0	0.0
Polygonaceae *Polygonum*........	2.30	1.0	0.0
Gramineae.....................	2.25	2.0	0.0
Labiatae......................	1.29	2.0	0.0
Cyperace......................	0.07	1.0	0.0
III. NO MACROSCOPIC PLANTS.......	*36.00*	*23.0*	*91.39*

[1] Indentification of the plants was made through the kindness of Corpora Billy G. Cumbie, Botanist, Tropical Research Medical Laboratory, U. S. Army San Juan, Puerto Rico.

Of the plants present in this stream, *Nitella* sp. appeared to be the one most frequently in association with the snail.

In an evaluation of the interspecies association of *A. glabratus* and other animals in the Sabana Llana, *Physa cubensis* and *Tropicorbis albicans* were found often in the same habitats with *A. glabratus*. Odds were about 1:1 for finding *A. glabratus* when *P. cubensis* and *T. albicans* were observed.

The opposite was true for Plecoptera and Simuliidae, for when these insects were present no *A. glabratus* were found because the water velocity was generally too great for the snail. No important relationship could be established between *A. glabratus* and other insects, mollusks, crustaceans, fish, and amphibians. Erdman (1947) has suggested that the guppy (*Lebistes reticulatus*) might be used as an indicator of conditions favorable for *A. glabratus*. Guppies were present in the Sabana Llana but, because of their great tolerance of a wide variety of environmental conditions, they are considered unreliable indicators of conditions favorable for the snail.

A. glabratus was not present in the Maracuta. Near the head of the stream, however, a few snails existed in a small spring-fed pool which at the time of this study did not serve as an infestation point for the stream.

The macroscopic fauna and flora were limited in number in the Maracuta while in the Sabana Llana these were abundant (Tables II and III).

TABLE III. The average number of macroscopic animals per square yard in the Quebrada Sabana Llana tributary and the Quebrada Maracuta

Animal	Sabana Llana Tributary	Maracuta
MOLLUSKS	6.420	0.003
Australorbis glabratus	4.220	0.000
Physa cubensis	1.220	0.003
Tropicorbis albicans	0.040	0.000
Ferrissia beaui	0.230	0.000
Potamopyrgus coronatus	0.650	0.000
Ampullaria sp.	0.060	0.000
INSECTS	1.523	7.181
Hemiptera	0.520	2.680
Trichoptera	0.060	0.050
Odonata	0.020	0.001
Coleoptera	0.040	0.000
Ephemerida	0.870	0.070
Diptera	0.010	0.410
Plecoptera	0.003	3.970
CRUSTACEANS	0.040	0.700
Decapoda		
Epilobocera	0.001	0.000
Shrimp (Misc)	0.040	0.070
ANNELIDS	0.001	0.000
Tubificidae	0.001	0.000
FISH	3.620	0.550
Teleostomi	3.620	0.550
AMPHIBIANS	1.000	3.250
Frogs (Misc)	1.000	3.250
TREMATODES	0.030	0.000
Monogena	0.030	0.000

The level of pollution in the Sabana Llana was classified as medium while that in the Maracuta was low. Although the pollution in the former stream provided organic enrichment for the growth of vegetation and animals, this factor probably was not the only reason for the differences in the organisms present in the 2 streams.

The vegetation on steep slopes surrounding the Maracuta is generally sparse. When it rains, large amounts of water collect rapidly in the stream, and the surge of water causes stones to roll and gravel to shift in the stream bed. Here the stream animal and plant life is frequently flushed and destroyed. As indicated in the Maracuta, only algae and animals such as insects, fish, shrimp, and other fairly agile species were able to survive. In contrast, the Sabana Llana collects water slowly because it has a relatively shallow drainage area. There, dense vegetation grows, prolonging the time during which the stream receives its water. These factors worked together to minimize the flushing and destruction of animals and plants in the Sabana Llana.

ISLAND-WIDE STUDY

Methods

The macroscopic fauna and flora at 421 stations well distributed over Puerto Rico were studied between March 1953 and May 1954. Sampling techniques similar to those of the previous study were used.

Results

The occurrence of macroscopic animals in habitats both with and without *A. glabratus* is shown in Table IV. The mollusks, *Ampullaria* sp. and *Marisa cornuarietis,* were found only where *A. glabratus* occurred. The distribution of both of these species, however, was limited to a few streams and rivers near San Martin and Caguas, so the presence of either of these 2 species cannot be considered a reliable indicator of habitats suitable for *A. glabratus. Ampullaria* sp. and *M. cornuarietis* are commonly used in aquaria and are considered recent introductions into Puerto Rico (van der Shalie 1948, Oliver-Gonzales *et al.* 1956).

Because both these species are new many parasites, predators, and other competitors normally present in their original habitats may not be present on the island. Therefore, with these natural limiting factors at a minimum these 2 species of snails might become abundant enough to replace *A. glabratus* as the dominant snail species in some of the water bodies in Puerto Rico. There are many reasons why this change may not occur. First, the most vital factor limiting the abundance of *A. glabratus,* as well as *Ampullaria* sp. and *M. cornuarietis,* is stream flushing, although the latter 2 were both found to be better adapted to resisting high water velocities than *A. glabratus.* For example, during May and June 1953 of the rainy season, the reduction in the populations of the 3 species on the Sabana Llana was as follows: 95%

TABLE IV. Animal occurrence in habitats with *Australorbis glabratus* and in habitats without this species in Puerto Rico at 263 stations surveyed from March through May, 1954. *A. glabratus* was present at 88 of the 263 stations

Animals	PERCENT with[a]	PERCENT without[b]
MOLLUSKS		
Physa cubensis	45.5	28.6
Tropicorbis riisei	10.2	11.4
Lymnaea spp.	9.1	6.1
Drepanotrema anatinum	6.8	2.3
Potamopyrgus coronatus	6.8	6.3
Ampullaria sp.	3.4	0.0
Tropicorbis albicans	2.3	2.9
Ferrissia beaui	1.1	1.7
Marisa cornuarietis	1.1	0.0
Melania sp.	1.1	0.6
Helisoma caribaeum	0.0	0.6
Tropicorbis decipens	0.0	2.3
Neritina spp.	0.0	2.3
INSECTS		
Ephemerida	59.1	46.8
Odonata	55.7	30.3
Hemiptera		
Belostomatidae	11.4	6.8
Corixidae	2.3	2.8
Notonectidae	1.1	6.1
Plecoptera	4.5	5.7
Coleoptera		
Dytiscidae	4.5	7.4
Larvae (unknown)	3.4	1.1
Hydrophilidae	1.1	1.1
Trichoptera (cases attached to stones)	3.4	10.3
Trichoptera (cases attached to organic material)	3.4	1.7
Diptera		
Simuliidae	1.1	2.9
Chironomidae	1.1	1.1
Culicidae	1.0	1.1
Tubifera	0.0	0.6
CRUSTACEANS		
Shrimp	6.8	29.1
Crab	1.1	1.1
ANNELIDS		
Tubificidae	1.1	4.0
FISHES		
Lebistes reticulatus	45.5	38.9
Unknown species	22.7	50.8
Poecilia vivipara	5.7	1.1
Xiphophorous helleri	1.1	1.7
AMPHIBIANS		
Frogs	13.6	9.1

[a] % of habitats with species shown and with *A. glabratus*.
[b] % of habitats with species shown and without *A. glabratus*.
Note: The difference between the sum of the percentages in the columns with footnotes a and b, and 100 %, represents the percentage of habitats without species shown.

for *A. glabratus;* 70% for *Ampullaria* sp.; 70% for *M. cornuarietis.* This difference in death rate between species does not favor the increase of *Ampullaria* sp. and *M. cornuariertis* because their potential rate of increase is much lower than that of *A. glabratus.* Also *A. glabratus* reproduces throughout the year while field observations indicate that reproduction in *Ampullaria* sp. and *M. cornuarietis* is limited to a few months in spring and summer.

While *Ampullaria* sp. and *M. cornuarietis* successfully occupy portions of habitats also occupied by *A. glabratus,* there are a number of differences in the ecology of the species which tend to minimize competition. For one thing, *A. glabratus* inhabits shallower water than either of the 2 larger species. *Ampullaria* sp. and *M. cornuarietis* are also positively rheotactic and generally are on the move upstream. *A. glabratus* seems to remain in the same pool or stream vicinity once it locates a suitable microenvironment (Pimentel *et al.* 1957). The evidence so far collected suggests that neither *Ampullaria* sp. nor *M. cornuarietis* under natural conditions in Puerto Rico will be responsible for the extermination of *A. glabratus.* Based on observations by one of the investigators (D. Pimentel) made in Venezuela where *A. glabratus* and *M. cornuarietis* have coexisted for many years, it is quite probable that the same will occur in Puerto Rico.

When *Physa cubensis, Lymnaea* spp., and *Drepanotrema anatinum* were present in a habitat the odds were substantially better than 1:1 that *A. glabratus* would also be present (Table IV). The presence of *Tropicorbis decipiens* and *Neritina* sp. definitely indicated habitats not suited for *A. glabratus* since the former lived in temporary bodies of water where *A. glabratus* was never found. *Neritina* sp. occurred in water which had a salinity too high for *A. glabratus.*

The ecology of *Tropicorbis riisei, T. albicans, Physa cubensis,* and *Lymnaea* spp. is similar enough to that of *A. glabratus* to have some competitive effect upon it. How important the influence of these species is upon limiting the abundance and distribution of *A. glabratus* is not known. *T. riisei,* in appearance, is strikingly similar to *A. glabratus,* so much so that the 2 species have been called one species by some workers. Morphological, physiological, and ecological differences can be established between them. Large populations of *T. riisei* were found in the semiarid region along the south coastal area of the island, whereas *A. glabratus* existed most often in the heavy-constant rainfall regions (Pimentel and White 1957). The 2 species often occurred together in the southeastern part of the island. *T. riisei* was a more effective competitor in the semiarid alluvial area of the south, primarily because it survived in swifter flowing water than *A. glabratus.* This was a factor of importance along the south coast where rainfall over a 7-month period caused severe stream flushing.

Certain insect groups were found associated with *A. glabratus* more often than others were (Table IV). The value of insects as indicators of habitats suitable for the snail is questionable because the distribution and numbers of insects changed rapidly, because of their vagility and their relatively short life cycle. Two insect groups, however, Trichoptera (cases attached to stones) and Simuliidae, were definite indicators of habitats where the snail was hardly ever found. These insects live in fast flowing water.

The Tubificidae inhabited water usually too polluted for *A. glabratus*.

The value of the crustaceans, fish, and amphibians as habitat indicators of *A. glabratus* is limited because they have a greater tolerance to various habitat factors than the snail has. However, as indicated, few *A. glabratus* were found to be associated with the shrimp group.

Parasites of *A. glabratus* are numerous but their precise influence on the snail has not been measured quantitatively (Faust and Hoffman 1934). These workers did show that single infections of *Schistosoma mansoni* were fatal to the snail in a few months; heavier infections killed more rapidly. In this study, the number of snails found destroyed by *S. mansoni* was small. In streams containing the parasite only about 5% of the snails were found infected. Other trematodes, such as *Cercaria marini,* for which *A. glabratus* acts as an intermediate host, may have similar effects. Double infections of both *S. mansoni* and *C. marini* were found in snails collected in Quebrada Barranquitas, but the exact effect of these infections on the total snail population is unknown.

Regarding predators, instances were observed in which the tree rat (*Rattus rattus*) had fished *A. glabratus* out of shallow pools consumed all but the shell. Rats were also seen feeding on snails which had become stranded on the stream bank after flood waters had receded. Scott (1942) reported that rodents consumed a large proportion of *A. glabratus* left stranded in a pond during a drought in Venezuela.

Frequently the fire ant (*Solenopis geminata*) and the crazy ant (*Paratrechina longicornis*) were observed killing stranded snails.

The occurrence of macroscopic plants in habitats with and without the snail is shown in Table V. No species of plant was found present in all the snail's habitats. The following plants, if present in a habitat, indicated at odds greater than 3:1 the existence of *A. glabratus: Nitella, Najas guadalupensis, Piaropus crassipes, Ceratophyllum dermersum* and *Commelina.* Other plants listed in Table V occurred frequently in *A. glabratus* habitats but were not reliable indicators.

TABLE V. Plant occurrence in habitats with *Australorbis glabratus* and in habitats without in Puerto Rico at 263 stations surveyed from March through May 1954. *A. glabratus* was present at 88 of the 263 stations

Plants	PERCENT*	
	with	without
SUBMERGED AND FLOATING		
Chlorophyceae (green algae)		
Hydrodictyon	2.3	0.0
Spirogyra	44.3	31.4
Cladophora	5.1	2.8
Rhodophyceae (red algae)		
Compsopogan	7.9	7.4
Ulvaceae		
Enteromorpha	0.0	1.1
Cyanophyceae (blue-green algae)		
Oscillatoria	6.8	3.4
Nostoc	4.5	1.1
Algae (Misc.)	5.1	8.0
Characeae (stone worts)		
Chara	4.5	2.3
Nitella	12.5	1.7
Salviniaceae (Salvinia family)		
Azolla carolininana	1.1	1.6
Salvinia sp.	0.0	1.1
Najadaceae (Pond weed family)		
Najas guadalupensis	30.7	7.4
Potamogeton spp.	4.5	3.4
Hydrocharitaceae (frog bit family)		
Vallisneria americana	1.1	0.0
Limnobium stoloniforum	4.5	1.1
Araceae (Arum family)		
Pistia stratiotes	2.3	0.0
Lemnaceae (Duckweed family)		
Lemna perpusilla	7.9	4.1
Spirodella polyrhiza	2.3	2.3
Ponterderiaceae (Pickerel-weed family)		
Piaropus crassipes	17.0	1.7
Ceratophyllaceae (Hornwart family)		
Ceratophyllum demersum	13.6	4.0
Nymphaeaceae (Water lily family)		
Nymphaea spp.	2.3	0.6
Schizomycetes (Bacteria)		
Sphaerotilus	1.1	3.4
EMERGENT AND ENCROACHING PLANTS		
Typhaceae (cattail family)		
Typha angustifolia	1.1	2.3
Commelinaceae (spider wort family)		
Commelina sp.	72.2	18.8
Cramineae (grass family)	54.5	61.1
Cyperaceae (sedge family)	5.7	12.0
Araceae (Arum family)		
Caladium	17.0	16.0
Alismaceae (water plantain family)		
Sagittaria spp.	6.4	5.1
Echinodorus cordifolius	2.3	0.0
Polygonaceae (Buckwheat family)		
Polygonum spp.	15.9	9.7
Umbelliferae (carrot family)		
Hydrocotyle spp.	4.9	1.1
Herbaceous	57.1	70.7

* Categories as in Table IV.

In a study to determine what effect the removal of vegetation would have on given snail population the Sabana Seca Canal was selected as the test habitat. Growing vegetations, in order of predominance were *Ceratophyllum demersum,* grass, *Piaropus crassipes,* and *Pistia stratiotes.* For 2 months weekly counts were made of the number of snails existing per sqaure pard at 20 stations along the canal. Then the floating, emergent, and encroaching vegetation was sprayed with 2-4-D, a chemical weed killer. The destroyed and submerged vegetation was dredged from the canal. About 25% of the snails were lost because they were removed with the vegetation. The chemical weed killer had no effect upon the snail itself. In addition, the snail population decreased 65%. This was attributed to the 8 inch drop in water level and the general upset of the natural environment caused by the removal of vegetation. Thus the total reduction in snail populations was 90% (Table II). In about 5 months, the vegetation was again choking the canal, but in regrowth the plants had changed order of predominance to *P. stratiotes,* grass, *P. crassipes,* and *C. demersum.* The snail population began increasing as the vegetation grew back. Rainfall was heavy during most of the regrowth period but its effect on snail abundance was considered negligible. The canal had an extremely low gradient (0.071%) and so flushing was not an important factor affecting the size of the snail population.

HABITS OF *A. glabratus*

Food

The snail was observed to consume varied types of organic material, excepting substances that were extremely hard in consistency. Both plant and animal life were utilized (Table VI). No particular plant seemed to be preferred over another. Although vegetation both in fresh and decayed state was eaten, decayed vegetation was preferred to fresh. In the laboratory, the snail would not feed upon fresh *Najas guadalupensis* even when it was the only food available, but would eat the plant in the decayed or cooked state. Most of the microscopic animal material consumed by the snail was in the decayed state. Animal wastes often were eaten.

TABLE VI. Organic material eaten by *A. glabratus*

Macroscopic Plants Both decayed and fresh	Plants Decayed Only	Macroscopic Animals Decayed	Animal Excreta
Lettuce	*Nitella*	*Bufo marinus*	Human
Cabbage	*Ceratophyllum demersum*	Tadpole	Hog
Water cress	*Chara*	*Lebistes reticulatus*	Cow
Algae	*Najas guadalupensis*	*A. glabratus*	Horse
Mangoes	*Caladium*		Dog
Mamey	*Piaropus cressipes*		Cat
Bread fruit	*Pistia stratiotes*		
Coconut	Tree leaves		
Potatoes	Coconut-palm fronds		

Observations suggested that plankton made up a large portion of the diet of the snail. Large populations of the snail existed in habitats where there was little macroscopic plant or animal life and no sewage. The snails in these habitats were probably feeding on the dead plankton adhering to the substrate.

Ability to Detect and Follow Receding Water

Field observations pointed to the fact that after severe floods anywhere from 10 to 20% of the *A. glabratus* population was left stranded on banks which had slopes of 20 degrees or less. A series of laboratory experiments was then undertaken to investigate further the ability of the snail to detect and follow receding water.

Laboratory environments simulating stream bottoms were constructed using pans (10 cm deep x 23 cm wide x 41 cm long) set at an incline of 15 degrees. Mud 2.5 cm deep was placed in the bottom of each pan and water added to a point where the mud at the shallow end was covered to a depthof 1.9 cm. Thirty snails (average 15.0 mm and range 9 to 12 mm) were placed at the shallow end of each of 12 pans. The snails were allowed 5 minutes to become accustomed to the new surroundings. In one group of 4 pans, the water was withdrawn at the rate of 0.32 cm in depth every 15 minutes until 1.6 cm of water remained at the lower end of the pan. In the second group of 4 pans, water was withdrawn at 0.32 cm every 4 minutes to simulate conditions of receding water on the Sabana Llana. In the third group of 4 pans, water was withdrawn at 0.32 cm every minute to simulate conditions on the Dona Ana, a stream which experienced frequent flushing.

The laboratory experimental conditions did not duplicate field conditions exactly, since the experimental situation consisted of a standing water environment instead of the flowing water of the actual streams. Even with this bias the laboratory experiments are considered valid for the following several reasons. First, the velocity of the water at the margin of the streams in the shallow water is near zero and characterized by slow moving eddy currents. Second, the snail occurs both in flowing and standing water habitats. Third, the investigators have observed snails in the stream margins being stranded as flood stages were receding.

Ninety-two percent of the snails followed water receding 0.32 cm in depth every 15 minutes, 34% at the rate of 0.32 cm every 4 minutes, 29% at a rate of 0.32 cm every minute. The small percentage that followed the quickly receding water did so by floating in it. Actually, snails of 15 mm diameter, as used in the test, move faster over a given surface than the rate of water recession in the 3 test situations. Laboratory observations indicated that the speed of movement of 10 mm and 20 mm snails over a silt-sand mixture averaged 50.2 mm and 125 mm per minute, respectively. *A. glabratus* are probably stranded not because they cannot move as fast as the water recedes but because they cannot detect and react quickly enough to these water changes.

Stranded snails move about at night when the humidity is high. Their success in locating water seems strictly due to chance, for as many snails have bene observed moving away as toward a given stream. Presumably a small percentage of the stranded population survive predators and desiccation until another flood stage covers them.

Aestivation

A. glabratus must endure desiccation when they are left stranded on the banks of streams after flooding or when the aquatic habitats disappear during a severe drought. Most investigators agree that *A. glabratus* can aestivate and so survive the infrequent drying of a permanent water body. Brumpt (1941) reported that a group of *A. glabratus* was maintained in a state of aestivation in the laboratory for 50 days with 48% of the 44 snails surviving. In Venezuela, Scott (1942) collected snails from a pond site which had been dry for 3 months and found that a "relatively small proportion of the snails survived the dry season." Olivier (1956) reported that *A. glabratus* survived almost complete desiccation over 7 months under laboratory conditions, and he also has evidence that in Brazil important strain differences exist in the species in its ability to survive out of water.

The aestivation of *A. glabratus* was studied in laboratory tests. In the first test, 250 ml beakers were filled three-fourths full with mud taken from a pool in a stream inhabited by *A. glabratus*. Enough stream water was added to bring the water level up to the surface of the mud. Ten *A. glabratus*, with an average maximum diameter of about 15 mm were placed into each of 82 beakers. The water was then allowed to evaporate and the snails were not fed. At weekly intervals thereafter, 4 beakers were withdrawn and the snails examined to determine the number alive. After examination of the sample, this group of 40 snails was discarded. The mud became hard and dry in 1½ weeks. No snails burrowed into the mud. Under these test conditions all the snails went into aestivation and one specimen survived for a maximum of 16 weeks (Table VII).

TABLE VII. Percentage of *A. glabratus* surviving in the laboratory on dry soil, based on successive weekly samples of 40 snails each

Weeks without food or water	Percent alive
1	37.5
2	65.0
3	52.5
4	30.0
5	10.0
6	30.0
7	17.5
8	10.0
9	5.0
10	5.0
11	2.5
12	2.5
13	2.5
14	2.5
15	0
16	2.5
17-20	0

In the second test, 10 snails were placed into each of 10 Petri dishes containing a 1.3 cm layer of mud. The soil was kept damp throughout the test period. No food was given to the snails. Once a week the snails were removed from Petri dishes and placed into a pan of water for 10 minutes to determine the number alive. The live snails were then returned to the mud. Under these conditions, one snail remained alive 11 weeks (Table VIII).

TABLE VIII. Percentage survival of 100 *A. glabratus* maintained in the laboratory on moist mud without food

Weeks without food	Percent alive
0	100.0
1	60.0
2	55.0
3	54.0
4	48.0
5	39.0
6	32.0
7	22.0
8	9.0
9	8.0
10	7.0
11	1.0
12	0

The third test was designed to measure the ability of *A. glabratus* to survive in water without food. Fifty snails were placed into each of 2 pans

(10 cm deep x 23 cm wide x 41 cm long). The water was changed every other day and the dead snails removed daily. Only 3 snails of the 100 were able to survive 4 weeks without food; by the fifth week all the nsails were dead (Table IX).

TABLE IX. Percentage survival of 100 *A. glabratus* maintained in the laboratory in water without food

Weeks without food	Percent alive
1	100
2	78
3	46
4	3
5	0

It seems highly probable that the presence of water prevented these snails from aestivating. Consequently they expended their energy and survived a shorter time than the specimens in the first 2 tests. The results of the third test might also explain why the snails in the second test did not live as long as the first group since they were brought out of aestivation when placed in water once a week during the study period.

Whether or not snails would burrow into mud and follow the water level during the evaporation process was also studied. One-gallon battery jars were filled three-fourths full with mud consisting mostly of clay and silt from a pool containing *A. glabratus*. Sufficient stream-tap water mixture was added to bring the water level 4.4 cm above the mud level. Twenty-five snails averaging about 17 mm in size were placed into each of 5 battery jars. No food was given to the snails. To speed the evaporation, a fan was directed over the battery jars. A week later only one of the 125 snails was found below the surface of the dried soil and it was located at the base of a crack where it may have fallen, not burrowed. Most of the dead snails were found partially imbedded in the soil, more a result of sinking into the soft mud than burrowing. An examination in the laboratory of snails in aestivation revealed the body retracted out-of-sight from the aperture. A dried mucous material had been secreted inside the shell close to the body all but sealing the snail body from outside exposure. These results are somewhat in contrast to those of Vilardi (1955) who reported that in laboratory experiments 20% of the snail populations burrowed into mud when water evaporated from their habitats. He also found that the snails did not follow the water level but burrowed into the mud just enough to cover their shells.

To determine if exposure to sun would force the snails to burrow into the mud when the water evaporated from the habitat, 75 snails averaging 15 mm in size were placed into each of 3 battery jars prepared by techniques similar to those used previously. These were placed in the sun. The snails were pushed 0.7 cm below the mud surface, and a fan was allowed to blow over the mud surface. Within 24 hours, 74 of the snails crawled out of the mud, the other one remained in the mud to dryness. Vilardi (1955) in a similar type of experiment placed snails 2.0 cf below the mud surface. He found in 10 days that 3 snails had crawled out of the mud and the 17 others in the experiment were dead, still buried in the mud.

In the field a search was made of the mud on the banks of streams where *A. glabratus* had been stranded. Snails were found only on the surface of the mud; none was below. These results agree with those of Brumpt (1941) and Scott (1942) but not with Barbosa and Dobbin (1952). However, further studies by Barbosa (1955) have revealed that *A. glabratus* was seldom found in mud and the few present in mud seem to have been passively buried.

Daily Migration

In the field, more snails were observed near the water surface during nighttime than during the daytime. Subsequently, this behavior was studied at the laboratory in an outside screen enclosure. Three aquaria 61 cm deep x 122 cm wide x 183 cm long) each with a dense growth of *N. guadalupensis* and each containing 500 snails averaging 12 mm (range 8 to 27 mm) in size were used. Observations on the distribution of the *A. glabratus* population were made at 30 minute intervals during a 24-hour period. Only snails which could be seen clearly at or near the surface were counted. The *N. guadalupensis* was not disturbed. At night, counts of the snails were made with a dimmed flashlight.

Few snails appeared at or near the surface during the daylight hours as compared with the large numbers present during the nighttime hours (Figure 3). Light is clearly an influencing factor, but the complete reason for the migration is not known.

SUMMARY

In this study on the biological environment and habits of *Australorbis glabratus* in Puerto Rico, it was found that:

1. The ecology of 2 species of recently introduced mollusks, *Ampullaria* sp. and *Marisa cornuarietis,* indicates that they probably will not markedly affect the abundance and distribution of *A. glabratus* in Puerto Rico.

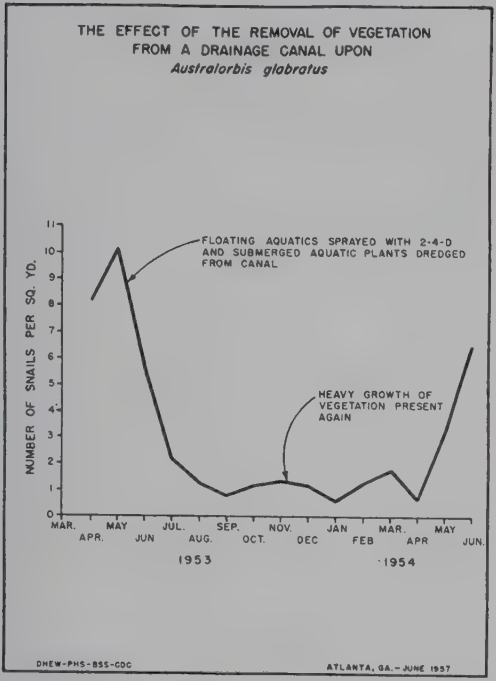


FIG. 2. The effect of the removal of vegetation from a drainage canal upon the *Australorbis glabratus* population. The number of snails counted weekly at 20 permanent stations and averaged for each month.

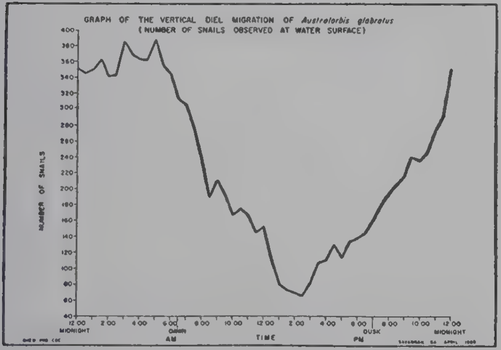


FIG. 3. The vertical diel migration of *Australorbis glabratus* (number of snails observed at water surface).

2. The snails, *Physa cubensis, Lymnaea* spp., and *Drepanotrema anatinum,* indicate the presence of *A. glabratus* at odds greater than 1:1.

3. Competition between *A. glabratus* and other species of snails having a similar ecology probably occurs but the degree to which they limit the abundance and distribution of *A. glabratus* is not known.

4. *Tropicorbis decipiens, Neritina* sp., Simuliidae, Trichóptera (cases attached to stones), and Tubificidae indicated habitats not suitable for the existence of *A. glabratus.*

5. Naturally occurring infections of *Schistosoma mansoni* occurred in only a small percentage of *A. glabratus.*

6. Rats and ants were observed killing many *A. glabratus* left stranded on stream banks after flushing.

7. The plants, *Nitella, Najas guadalupensis, Piaropus crassipes, Ceratophyllum demersum,* and *Commelina* indicated the presence of *A. glabratus* at odds greater than 3 to 1.

8. In one stream the removal of vegetation caused a 90% reduction in the snail population.

9. The food consumed by *A. glabratus* consisted of many types of living and decayed organisms.

10. In laboratory tests, the rate of movement of snails 10 mm in diameter was 5 cm per minute and for snails 20 mm in diameter 12.5 cm per minute.

11. Many *A. glabratus* were observed stranded by receding water on stream banks with slopes of 20 degrees or less. Although the snails could move faster than the water receded, they were stranded because they could either not detect or respond to the water level changes.

12. In the laboratory, a small percentage of *A. glabratus* resisted desiccation by aestivating for as long as 4 months. They did not burrow into mud to aestivate.

13. In the laboratory *A. glabratus* was observed to have a vertical diel migration to the water surface at night and deep in the water during the daytime. This substantiated field observations.

Acknowledgment

The authors wish to thank Mr. Victor Ildefonso, Mr. Rolando Cancel, and Mrs. Aida Z. de Colon for their technical assistance in making many of the routine observations.

REFERENCES

Barbosa, F. S. 1955. Personal communication, June 1, 1955.

——— **and J. E. Dobbin.** 1952. Effects of the dry seasonal on *Australorbis glabratus* (Mollusca, Planorbidae). Pub. Avulsas do Inst. Ag. Mag. **1:** 145-147.

Brumpt, E. 1941. Observations biologiques diverses concernant *Planorbis (Australorbis) glabratus* hote intermediaire de *Schistosoma mansoni.* Ann. De Parasit. **18:** 9-44.

Erdman, D. S. 1947. Aquarium fishes in Puerto Rico. Rev. de Agr. de P. R. **38:** 90-91.

Faust, E. C., and W. A. Hoffman. 1934. Studies on schistosomiasis mansoni in Puerto Rico. III. Biological Studies. I. The extra-mammalian phases of the life cycle. Puerto Rico J. Pub. Health and Trop. Med. **10:** 1-97; 133-245.

Myerhoff, H. A. 1933. The geology of Puerto Rico. Mon. Univ. of Puerto Rico. Ser. B., No. 1.

Oliver-Gonzales, J., P. M. Bauman, and A. S. Benenson. 1956. The effect of the snail *Marisa cornuarietis* on *Australorbis glabratus* in natural bodies of water in Puerto Rico. Amer. J. Trop. Med. and Hygiene, **5:** 290-296.

Olivier, L. 1956. Observations on vectors of Schistosomiasis mansoni kept out of water in the laboratory. J. Parasit. **42:** 137-146.

Pico, Rafael. 1950. The geographic regions of Puerto Rico. Univ. of Puerto Rico Press. Rio Piedras, Puerto Rico.

Pimentel, D. 1957. Life history of *Australorbis glabratus,* the snail intermediate host of *Schistosoma mansoni* in Puerto Rico. Ecology, **38:** 576-580.

——— **and P. C. White, Jr.** 1957. a. Geographic distribution of *Australorbis glabratus,* the snail intermediate host of *Schistosoma mansoni* in Puerto Rico. Jour. Trop. Med. and Hygiene, **6:** 1087-1096.

———. 1959a. Physiochemical environment of *Australorbis glabratus,* the snail intermediate host of *Schistosoma mansoni* in Puerto Rico. Ecology **40:** 533-541.

——— **and Victor Ildefonso.** 1957. Vagility of *Australorbis glabratus,* the snail intermediate host of *Schistosoma mansoni* in Puerto Rico. Amer. J. Trop. Med. and Hygiene, **6:** 576-580.

Scott, J. A. 1942. Epidemiology of schistosomiasis in Venezuela. Amer. J. Hygiene, **35:** 337-367.

Van der Schalie, H. 1948. The land and fresh-water mollusks of Puerto Rico. Misc. Publ. Mus. Zool. Univ. of Mich., No. 70.

Vilardi, A. D. 1955. Personal communication. May 31, 1955. In personal communication through J. A. Jove, May 31, 1955.

THE PHYSICAL ENVIRONMENT OF SOIL ANIMALS

N. Collis-George
School of Agriculture, University of Sydney, N.S.W.

Introduction

There is little experimental evidence of the physical requirements of soil animals, although a great deal of qualitative information about the habitats of the major groups of soil animals has been recorded, *e.g.* Kevan (1955). From a consideration of the properties of soils, it is possible to deduce quantitatively the range of ennvironmental conditions that can arise, and to specify the actual environment that an organism is enjoying from a definition of the soil conditions in which it is normally found. It is not proposed, in this discussion, to consider the chemical and nutritional aspects of the soil environment, even though they have a very marked influence on animal distribution. In this restricted sense, we are effectively assuming that no limitation on distribution is imposed by these two factors, and that the physical environment is limiting. The soil, as a region inhabited by plants and animals, can be considered as composed of the pores between the mineral and organic particles and of the surface of these pores.

The *structure*[1] of the soil can be regarded as consisting of two independent systems, firstly as a labyrinth of interconnected pores, and secondly as an "edifice" of contiguous solid mineral particles. The Biologist is concerned with the former description, and can usually ignore the exact chemical and mineralogical description of the edifice. Unfortunately, it is much easier to visualise the arrangement of *ultimate particles,* i.e. in the finest state of subdivision, and of the *aggregates* compounded of ultimate particles, than it is to visualise the pore arrangement and this has led to the description of the soil in terms of *texture* in most biological work.

Limiting our discussion to the pores and pore surfaces inhabited by animals, the principal physical environmental factors that control their behaviour may be treated under 4 headings: the soil water in terms of supply; the soil atmosphere as it controls the oxygen/carbon dioxide balance in the air and water-filled pores; the soil temperature; and a complex factor concerned with the freedom of movement of the animal.

Soil Water

The amount of soil water greatly influences the other environmental factors, and to appreciate its overall importance it becomes necessary to consider the energy/moisture-content relationship in some detail.

Mathematical consideration of the structures of ideal systems composed of identical spheres, indicates that, regardless of the packing arrangement, the pores are of complex shape. Each pore is connected to several neighbors, never less than four, by necks of smaller dimension than any other dimension of the pore. In soils, the particles are not spheres, and their sizes vary from ultimate particles of about 0.01, inch in thickness, to gravel. In addition there are aggregates of all sizes each with an internal pore size distribution. The arrangement of ultimate particles and aggregates can produce very varied pore systems from long continuous cracks to microscopic cul-de-sacs. The characteristic of the pore systems obtained from arrangements of granules, *e.g.* the seed bed condition of a cultivated soil or of loose sands, is that the entry neck of each pore is smaller than the pore itself. Consequently, when water is removed from such a system by drainage, a pore can only drain if the air-water interface is able to enter by some neck. This is analogous to the capillary tube phenomenon of water rising up a tube from a flat water surface, against gravitational forces acting downwards. The air-water meniscus can only pass through the neck and empty the pore, if the force applied is greater than the equivalent surface tension force; the bigger the pore neck, the easier it is to drain the pore.

---

[1] Italicized terms are in common use in Soil Science and have the restricted significance indicated in the text. A general discussion of Soil Physical properties can be found in Baver (1956).

In those soils, where large continuous cracks due to soil genetic weathering processes, or where long cavities caused by decaying roots of the passage of animals occur, the same principles apply, and these elongated or flattened pores can only remain full of water if the force applied to the soil water is smaller than the maximum surface tension force derived from their geometry. In the case of worm holes and cracks 3 mm in section this would mean they would only remain full of water 1 cm above the soil water table, and that for all practical purposes these large "pores" will only be water filled when the soil is waterlogged.

In addition to this capillarity phenomenon, the osmotic pressure of the soil solution, and the diffuse ionic layer of the colloidal particles exert a force retaining soil water against external agencies. Furthermore, the ubiquitous phenomenon of surface absorption tends to maintain thin films of water on soil surfaces, when the forces removing soil water are greater than the pore neck size, or the concentration of ions, can withstand. This last phenomenon is well outside the limit of forces normally exerted by animals or plants, and can be ignored in this context.

The energy required to remove water from a soil, therefore, depends on: (1) the types and relative numbers of ultimate particles, *texture;* (2) the arrangement of these particles and their aggregates, *structure;* (3) the concentration of ions in the soil solution.

Figure 1 illustrates energy/moisture content relationships, i.e. *moisture characteristics,* obtained by techniques in vogue in soil science, on soil types with low salt concentrations. The water energy at a particular moisture content is equated to the work required to remove 1 cc from an infinite volume of soil (so that there is no change in moisture content) to a mass of free water at zero energy. The zero of energy is equated to that of a flat water surface in equilibrium with atmospheric pressure (*Water-table*).

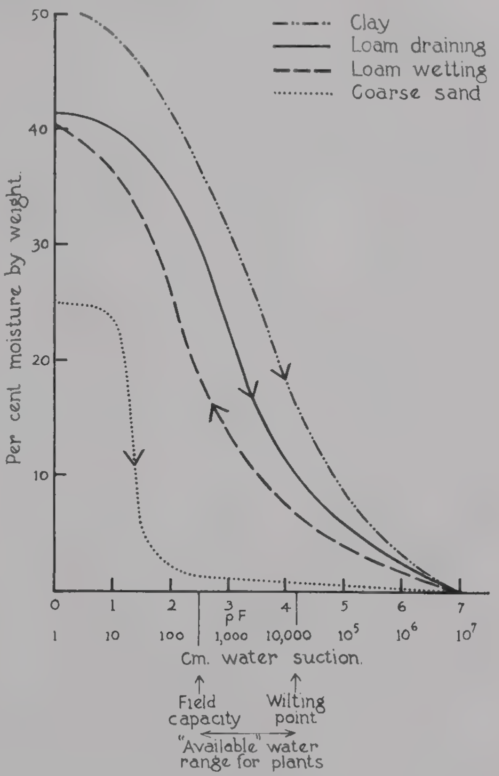


FIG. 1. The moisture characteristics of 3 soil materials.

The unit of erg/cc is too small for practical purposes and is replaced by the unit of cm water *suction* (negative pressure), where 981 ergs/cc are equivalent to 1 cm water. For complete moisture characteristics, a logarithmic scale of suction, the *pF* scale, is employed. The curves in Figure 1, on a pF scale, commence with a suction of 1 cm and the very large pores (> 3 mm) due to cultivation (animals and roots) are not included, whilst all smaller pores whatever their geometry are included. Normally these curves are produced by suction techniques (Childs and Collis-George 1950) and it is not convenient to examine the water retaining powers of pores which are of the same order of magnitude as the thickness of the sample under examination. Definition of these large pores is most easily made by the optical techniques of Kubiena (1938). However, since the larger pores can only remain full of water at very low suctions, their exclusion from the curves of Figure 1 would only assume importance in waterlogged materials when the soil water energy is zero.

Figure 1 shows that the energy needed to remove water from a drying soil increases the drier the soil becomes; consequently, to obtain water the animal has to perform work at least equal to the energy retaining water in the soil. With most agricultural plants it is observed that permanent wilting occurs when the suction in the main soil mass is approximately 15,000 cm water (pF 4.2). The free energy of soil water at wilting point, moreover, corresponds to a relative humidity of 98.5%, which would imply that the majority of soil animals living in association with plants have a very low relative humidity tolerance. The measurement of relative humidity, however, particularly in the range 100-98%, is not very easy or accurate and therefore the definition of the soil water energy in terms of suction is much more amenable to interpretation than is relative humidity.

The energy relationship generally ignores the actual salt regime of the soil, since osmotic pressures are small (about 200 cm) for soil solutions weaker than 200 ppm. For more saline soils, the osmotic effect, being additive to the surface tension effect to give the total soil water energy, causes plants to wilt at higher moisture contents.

When an animal is placed in a dry porous system, water will flow from it into the soil unless the osmotic pressure of its body fluid is equal to the energy of the soil water; if not, to prevent desiccation, the animal must either expend work and increase the free energy of its own body fluid to that of the soil water, or form some impermeable outer covering to prevent water loss. The water movement is not necessarily restricted to liquid transfer; at higher suctions, vapour movement is probably dominant.

At midday with a drying wind, the relative humidity at the surface of the soil may be as low as 50% (pF 6), and it is to be presumed that any soft-bodied animal without a waxy outer layer would desiccate. In lower horizons of the soil profile, the suction in equilibrium with relative humidity would be less, but may approach pF 4.2. Under these conditions, many animals probably migrate still deeper into the soil (*e.g.* earthworms and wireworms, Lees 1943) or change into less active and more resistant forms to maintain their water content (*e.g.* bacteria), or perhaps have a physiological mechanism of producing water by oxidation of foodstuffs similar to that possessed by stored product pests. Wigglesworth (1948) has suggested that insect cuticles, whilst waxed to resist vapour diffusion losses, are constantly abraded by soil particles. On the other hand, many insects seem able to withstand very low relative humidities of 85% without loss, so that abrasion in the lower horizons of soil will not usually be of the same significance as in the upper layers.

For animals able to reach the surface, dew at almost zero energy can be obtained in the night hours. Parry (1954) has suggested that spiders, which were unable to either drink from porous media with full pores if the suction was 600 cm water (pF 2.8), or from systems with pores empty at even lower energies, obtain their water from dew when soil is drier than these limits. A phenomenon has been observed by Collis-George and Blake (1959) concerning the "hatching" of *Anguina agrostis* galls. The galls swelled and ejected their larvae the more easily the lower the suction. It is interesting to note that at 600 cm water suction (pF 2.8) only 10% of galls were effective; by varying the "soil media," it was shown that even at very low suctions, if the majority of pores were empty, the nematode larvae did not emerge.

A summer shower usually wets the surface to a shallow depth only, and the suction, except in the first day after the shower, soon rises as plant transpiration and evaporation occur. In the seasons when rainfall exceeds evaporation, the moisture content may rise to saturation, but if drainage under gravity to a deep water table is able to occur, water contents corresponding to suctions of about pF 2.5 *field capacity,* result. In the wetter periods, therefore, the moisture energy is often about pF 2.5; and only infrequently are suctions consistently lower than 300 cm water, except in sites with bad drainage,; in the dry periods, pF is usually greater than 2.5 and occasionally greater than 4.2. Soil organisms, therefore, would be expected to have physiological mechanisms permitting either tolerance of these extremes of conditions, or removal actively or passively from some seasonal environment. At high suctions the animal has the ability either to obtain water against these suctions, or to withstand desiccation and await the temporary periods of low energy, dew formation or showers; at the low suctions associated with waterlogging and land drains running, the animal has either to resist absorption caused by osmosis, or, if unable to do this, to excrete water to keep up the body-cell osmotic pressure. The energy requirements of animals, and therefore their distribution, could be expected to be different in sites of rapid drainage as compared with imperfectly drained sites, where the moisture regime remains wetter than pF 2.5 for extended periods of each year.

It is now clear that when experiments are designed to study the relationships between the animal and the water regime in real or artificial soils, the results will only be interpretable if the soil water suction is controlled and the moisture characteristics (*i.e.* a measure of structure) known for each medium. Measurements of water content, in terms of saturation content alone, can only be misleading, since not only is the % saturation nonlinearly related to suction, but the meaning of saturation itself is vague in swelling materials like soils. Thus in clay soils (*e.g.* in Fig. 1) the change in moisture content, once the large cracks and worm holes have emptied at the lower suctions, is mainly caused by pores shrinking but remaining full of water, with no consequent increase in air content, as compared with the pore emptying in a semi-rigid medium like sandy soil.

In experiments at various moisture regimes, it is necessary to have thin samples or to have complex equipment to ensure uniform moisture content and suction throughout the experimental area, as it is a well substantiated fact that considerable gradients can remain almost indefinitely in soils where the majority of pores have been emptied.

There is, in addition, another phenomenon associated with soil water which requires consideration in the design of experiments, that is, that the shape of the moisture characteristic is considerably modified by the previous wetting history of the soil. Thus the suction at a particular moisture content is dependent on whether the soil is wetting or drying. The extreme relationships are derived starting from a water-logged soil in one case and from an oven-dried soil (approx. pF 7) in the other (dotted line in Fig. 1 for the loam soil) and form the *hysteresis* envelope. If the previous wetting history is unknown, the suction can lie anywhere within the limits of the hysteresis envelope. This particular complication has not been included in the example given at the conclusion of this paper.

Soil Atmosphere

The partial pressure of oxygen in the soil atmosphere is closely controlled by the ease of diffusion from the external atmosphere through the soil; similarly, the partial pressure of carbon dioxide is controlled by the ease of access to the surface. It would be expected that when the pathways through the soil are narrow and tortuous, there would tend to be a high CO_2/O_2 ratio increasing with depth. This ratio would decrease as the pores became larger and the pathways straighter. It has been shown, however, that over a wide range of air—water ratios in the soil, the diffusion coefficient is a linear function of the air porosity and independent of the type of soil (Penman 1940); such that generally for air porosities greater than 10% by volume, the rate of exchange of oxygen and carbon dioxide with the surface atmosphere comes to equilibrium to depths of 30 cm in periods of one hour. The ratio of CO_2/O_2 increases (1) with increase in depth and (2) with decrease in air porosity. The sum of the O_2 and CO_2 concentrations remains very nearly constant at 21%.

When the water content is increased and the pore air volume is less than 10%, the simple diffusion relationship becomes invalid and the type of soil, *i.e.* the tortuosity of the remaining air-filled pores becomes more important, and the concentration gradients become such that the O_2 concentration approaches zero. Similarly CO_2/O_2 ratio in the soil water is controlled by the soil atmosphere in contact with it. Diffusion of gas molecules in water is slower than in gases, so that at small distances below the air-water interface the rate of O_2 supply, as well as O_2 concentration, will approach zero unless there is some bacterial source of O_2, as in paddy soils. The distribution and activity of animals, as a consequence of CO_2/O_2 ratio and O_2 requirements, in the air and water filled pores, will therefore be closely controlled by the water content of the soil, itself a function of the structure and suction.

A further aspect of the soil atmosphere of importance to the animal is the relative humidity already mentioned under SOIL WATER. In a soil where plants are still functioning (*i.e.* not wilted) the root neighborhood has a pF of less than 4.20 and consequently a relative humidity of more than 98.5%, with a consequent loss by diffusion to a drier atmosphere above the soil surface. However, very slight variations in relative humidity from 100 to 98.5%, due to temperature and climatological changes, correspond to very great variations in the efficacy of the atmosphere as a desiccating agent. It is of interest to examine the order of events after a very simple temperature change. Suppose a soil is at temperature T_1, moisture content Θ_1, and suction S_1 in equilibrium with a vapour pressure p_1 since the free energy of the water vapour (in equilibrium with S_1) is defined by p_1/p_{10}, where p_{10} is the saturation vapour pressure at T_1.

If now the temperature is suddenly raised and kept at T_2, momentarily the relative humidity p_1/p_{20} is lowered and corresponds to a free energy greatly in excess of S_1. Water now begins to distil from the soil and the organisms in the soil, until a new relative humidity p_2/p_{20} is reached in equilibrium with an increased S_2 and a decreased moisture content Θ_2.

On suddenly lowering the temperature to T_3, the relative humidity p_2/p_{30} is greatly in excess for equilibrium with S_2 and water vapour condenses on the soil and the soil organisms until a new stage of equilibrium p_3/p_{30} is greatly in excess for equilibrium with S_2 and water vapour condenses on the soil and the soil organisms until a new stage of equilibrium p_3/p_{30}, S_3 and Θ_3 (now the "wetting" moisture characteristic) is reached.

The amplitude of the variations in p, S and Θ will depend on the ratio of the volume of soil air and total moisture content in the soil.

Diagrammatically, this sequence of events for a 2 degree fluctuation is represented in Figure 2, for a closed soil-water air system isolated from the above-ground atmosphere. The points marked X, on S and Θ curves, indicate the relative equilibrium values (that are never attained) created by the temporary relative humidity of p_1/p_{20}, and similarly the points marked Y refer to the temporary relative humidity of p_2/p_{30}. For an animal to transpire water into the soil atmosphere, the vapour pressure in its respiratory tract has to be greater than in the main soil mass. If the animal is in equilibrium with the free energy of the soil water, respiration can only be achieved by raising its body temperature above that of the soil mass. For animals at or near the surface, temperature and relative humidity changes will be quick and of large amplitude, as compared with positions remote from the soil surface. A continuous diurnal change rather than the step-like succession of T_1 to T_3 will occur, with, additionally, the superimposition of changes in soil moisture content due to rainfall and transpiration and quick changes in the soil's relative humidity by diffusion in response to aerial humidity fluctuations. These will cause the soil atmosphere vapor pressure to fluctuate and must subject the animal's respiratory mechanism to desiccating and "drowning" effects within relatively short periods of time, unless the animal's temperature control is very exact.

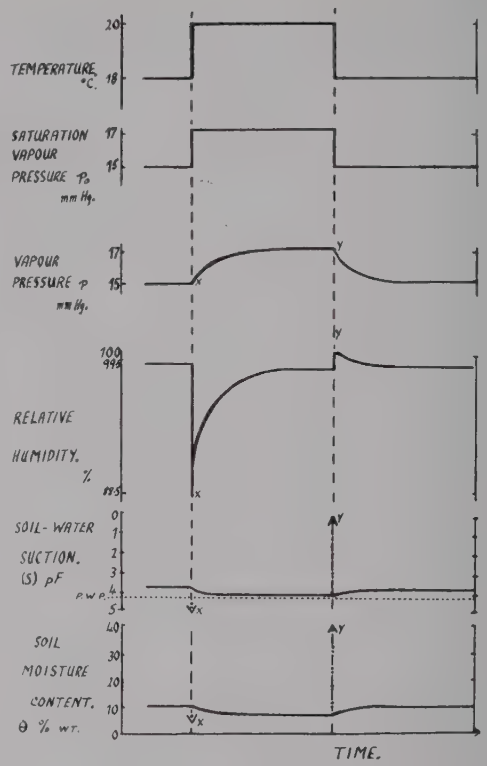


FIG. 8. Fluctuations in soil moisture content, suction, and vapor pressure consequent on abrupt changes in temperature in a soil-water system.

The sensitivity of animals to relative humidity changes would be expected to govern their distribution in the soil profile.

SOIL TEMPERATURE

Records of the variation of soil temperature with season, latitude, cover, and depth have been published in detail. Besides the general temperature sequence to be expected from these records in a given locality, the type of soil also has an effect, particularly in relation to its moisture content.

The specific heat of most dry soils is about 0.2 cals/gm, thus as the water content increases so is there a linear increase in thermal capacity with a consequent smaller rise in temperature in a given layer of soil exposed to the sun. In addition the thermal conductivity of a wet soil is greater than that of a dry soil, consequently temperature gradients over a column of wet soil are smaller than those over a dry one for the same heat input at the surface. The interaction of thermal conductivity and thermal capacity, both dependent on water content, cause a wet soil in spring sunshine to be cooler at the surface but warmer at depth than the same soil when drained. An animal on the surface would experience higher temperatures than the soil it moved over if it had a smaller area in contact with the soil than the area exposed to sunlight. A cultivated soil having a seed bed tilth would be warmer than an uncultivated soil because it has a dryer surface, and because it is discontinuous from the subsoil. This might account for the activity in early spring of such pests as flea beetles (*Phyllotreta* spp.) and pea and bean weavils (*Sitona* spp.)

Chemical reaction rates increase approximately twofold for a 10°C rise in temperature, and the rate of rise of temperature and its fall in autumn at different depths from the surface, and at different moisture contents, must be expected to cause organisms with differing physiological processes to be selectively activated. Some *Lumbricus* spp. for instance, are unable to withstand high temperatures of 26°C and are found to migrate to cooler depths even in moist soils in South Australia. Animals therefore would be expected to migrate vertically with seasonal changes, or to have other means of accommodation to temperature changes, *e.g.* dormancy of the beet eelworm (Jones 1950).

Freedom of Movement

Under this factor animals fall into two main divisions, firstly those that are able to burrow or, in some way, alter the existing geometry of the soil, and secondly those which are unable to change the structure and with their movement confined to the existing cavities of the soil.

Animals that move the soil will be affected by several soil physical properties as regards their population density, just as much as by chemical factors. The principal property is the strength of the soil to resist deformation, *i.e.* shear strength, whether the animal bites, levers, pushes, or scrapes its way. The more moist the soil, the lower the shear strength, with consequent reduction in the work requirement of the animal. However, reduction in shear strength might cause collapse of the newly made passages as the very wet soils become plastic. Another property to be considered is adhesion, which is very small in dry soils and reaches a maximum in the region of field capacity, at the so-called sticky point. Thus, although shear strength is decreasing with increase in moisture content, the stickiness is increasing and the animal will have to expend more work on overcoming friction. Finally, a soil property independent of moisture content, namely texture, inhibits some organisms like earth worms if the soil is sandy, and especially if the coarse sand particles are angular and sharp-edged. The thicker the water films, the less important the abrasive aspect of angularity of particles becomes.

For smaller animals, such as nematodes restricted to the existing pores, the structure of the soil is the prime consideration. The moisture characteristic is of special importance, as the smallest dimension of each pore is related to the suction required to empty it of water. For rigid systems a pore that empties at pF 1 would have a neck radius of about 150μ, at pF 2 of about 15μ, etc. For shrinking systems, the moisture characteristic cannot be interpreted in terms of pore emptying unless a shrinkage moisture content relationship is also determined; *e.g.* a laboratory specimen of Kaolinitic clay would empty its pores when they had contracted to an equivalent pore neck radius of 1μ, at a moisture content of 30% by weight and pF 3.2; consequently, at a moisture content of 50% at pF 2, the pore neck radius from geometrical considerations would be about 1.3μ, or some 10 times smaller than pores which empty at pF 2 in a completely rigid system.

Information on field soils is restricted on this topic, but there seems little doubt that pore dimensions available to soil animals requiring water to move in will lie within narrow limits in most soils. When a pore is emptied, there are still films of water on the walls, and in lenses where various particles touch. The thickness of films on the surface is, however, very small, even at low suctions, and decreases with increase of suction. On mica, a mineral with a surface similar to many soil minerals, water films on flat surfaces have been shown to be 0.05μ at pF 1 (Schofield 1946). Hence movement within films by animals becomes inadmissable. The lens between particles has a concave surface with radius controlled by the suction and the particle sizes, so that a coarse textured soil has lenses more isolated from one another than a finer textured soil at the same suction. It would be expected that a comparatively low suction, when pores are emptied and lenses isolated, coarse sandy soils would not allow movement of animals which require a water environment. This type of phenomenon has been observed with the stem eelworm *D. dipsaci* by Wallace (1955).

Discussion

At any given geographical locality defined in terms of latitude, aspect, altitude, etc. the physical properties of the soil, which, in their interaction, decide the environment at a particular depth in the soil, are thus (a) the texture, (b) the structure, and (c) the soil-water suction. The first property is hardly variable in any situation and can be determined by simple assessment. The second property is a reflection of time (soil weathering process) vegetation, cultivation, climate, soil fauna and of the texture. The structure must therefore vary with depth. Its measurement in the present context would be best carried out as a moisture characteristic and by direct examination for the larger pores. The third quantity, the suction, is a consequence of the water regime that the soil has experienced in terms of depletion (by drainage, evaporation and transpiration), accretion (by rainfall and artesian water) and the amount of water in the soil. The number of pores filled and empty of water is a reflection of the structure, and is to be determined by combination of moisture content/volume and moisture content/suction relationships.

The 4 environmental factors that have been discussed are all consequences of the above 3 physical properties to varying degrees. The environmental factor of greatest importance is undoubtedly the moisture content as it, in turn, controls the others. The moisture content, however, cannot be adequately specified as a percentage and its definition in terms of the moisture characteristic is required if the environment of the animal is to be described. The soil-water suction would normally include the osmotic pressure contribution, as this is small in most soils. In saline soils or in other abnormal conditions, the contribution of osmotic pressure to pF would also be required.

In experimental work designed to elucidate the range of environmental conditions in which a soil animal can function, the specification of temperature, humidity, CO_2 O_2 ratio, freedom of movement, in terms of moisture content, for one soil site under given climatic conditions, can only be transposed to other soils if the soil physical properties are defined.

Suppose a nematode, diameter 20μ, investigated in a sand similar to that of Figure 1, was found not to lose body water up to pF 3; to have a sufficiency of oxygen at 22% moisture content, pF 1.2; an optimum temperature of 25°C; and freedom of movement up to pF 1.5. The optimum physical environment for this animal in this sand would be between pF 1.2 and 1.5 or between 22% and 5% moisture content. (For results similar to this model see Wallace (1956).

Transposing this to the drainage curve of the loam soil in Figure 1 the following conditions are required to give a similar physical environment: water supply would still be limiting at pF 3; the oxygen requirement, satisfied by 20% water in the sand, corresponds to an air porosity of 9.3% by volume and is satisfied by the loam at 35%[2] water, pF 2; the optimum temperature would be constant, but it would occur later in the season because of the time to drain to the same thermal capacity, and because of the enhanced thermal conductivity. A circular cross section of the diameter of 20μ corresponds to pores emptying at pF 2.2 in a rigid material. In the loam, an incompletely rigid material, many of the pore necks would be smaller than 20μ diameter at pF 2.2, and migration would cease at about pF 2.2, if the nematode had a rigid circular cross section of 20μ. The optimum physical environment would thus lie between pF 2.0 and 2.2 or between 35 and 33% moisture. If the nematode can squeeze through a neck of 5μ, the limits would lie between pF 2.0 and 2.8, 35 to 26% moisture. If the animal is able to wriggle through one water lens to the next without the cells themselves being full of water, the limit to migration in terms of moisture content is equivalent to a greater suction, and before it become operative, the water supply factor at pF 3.0 would limit the environment; the environmental limits would then lie between pf 2.0 and 3.0, 35 and 23% moisture.

This example, based on very tenuous assumptions and for a hypothetical animal, neverthless indicates that the interaction of the environmental factors can make the limits of moisture content differ in various soils for the same animal.

In qualitative terms, the physical environment of the major groups of soil animals are described by the various contributors to Kevan (1955). These authors and, in particular, J. Gordon Blower on "Millipedes and Centipedes as soil animals," provide detailed but subjective evidence, which in the light of this discussion, serves to emphasise the necessity of defining the soil physical environmental factors exactly.

Conclusions and Summary

This theoretical study suggests that, to establish the environmental requirements of soil inhabiting animals, the indirectly controlled environmental conditions created by the physical properties of the particular soil of any investigation must be defined, as well as the conventional measures of external environment such as moisture content.

It would appear possible to define the optimal environment of the animal in one physical medium, in terms of temperature and soil moisture suction (pF), and to transfer the requirements to another soil of known physical properties.

---

[2] The transposition of weights to volumes and back again makes use of the true specific gravity of the soil solids which is 2.6 for many soils.

The most important of the environmental factors controlling the physical behaviour of soil animals is soil-water, which largely dominates the other aspects of the environment, namely soil atmosphere, soil temperature, and freedom of movement. These factors are controlled by 3 soil physical properties, *texture, structure* and *soil-water suction;* and one mechanical property, the *shear strength,* which is moisture dependent.

REFERENCES

Baver, L. D. 1956. Soil Physics. 3rd Ed. New York, Wiley.

Childs, E. C. and N. Collis-George. 1950. The Control of Soil Water. Adv. in Agron. 3: 233.

Collis-George, N. and C. D. Blake. 1959. The influence of the Soil Moisture regime on emergence of larval of the nematode *Aguina agrostis.* Australian J. Biol. Sci. 12: 247-256.

Jones, F. G. W. 1950. Observations on the beet eelworm and other cyst-forming species of *Heterodera.* Ann. Appl. Biol. 37, 407.

Kevan, D. K. McE. (Editor). 1955. Soil Zoology. London, Butterworths.

Kubiena, W. 1938. Micropedology. Ames, Iowa, Collegiate Press.

Lees, A. D. 1943. On the behavior of wireworms of the genus *Agriotes esch.* (Coleoptera, Elateridae). I. Reactions to Humidity. J. Exptl. Biol. 20: 43.

Parry, D. A. 1954. On the drinking of soil capillary water by spiders. J. Exptl. Biol. 31: 218.

Penman, H. L. 1940. Gas and water movements in soils. J. Agric. Sci. 30: 437.

Schofield, R. K. 1946. Ionic forces in thick films of liquid between charged surfaces. Trans. Faraday Soc. 42B: 219.

Wallace, H. R. 1955. The influence of soil moisture on the emergence of larvae from cysts of the beet eelworm. Ann. Appl. Biol. 43: 477-484.

———. 1956. The effect of soil structure on the emergence of larvae from cysts of the beet eelworm. Nematologia 1: 145-146.

Wigglesworth, V. B. 1948. The insect cuticle as a living system. Disc. Faraday Soc. 3: 172.

THE DISTRIBUTION AND DYNAMICS OF SOME FOREST SOIL MITES

JOHN A. WALLWORK[1]
Zoology Department, University of Michigan

INTRODUCTION

Published studies on the biology of forest soil mites in the United States are few. The contributions of Jacot (1936, 1939, 1940), Eaton and Chandler (1942), Pearse (1946) and more recently, Birch and Clark (1953), Bellinger (1954), and Hairston and Byers (1954), have drawn attention to some of the factors affecting micro-arthropod populations in the soil. The lack of adequate taxonomic descriptions of even the more common soil mites has hampered very greatly the work of the soil zoologist. More results are available from Europe where the fauna is better known, and van der Drift (1951) has summarized much of this work. Among the many noteworthy contributions may be included those of Tragardh (1929), Haarløv (1942), Weis-Fogh (1948), Fenton (1947), Forsslund (1948), Evans (1951). However, much of the work has been devoted to comprehensive surveys of the mesofaunal elements of the soil, and less attention has been paid to the behavior and effect of individual species.

This paper describes some ecological observations on the mite and collembolan fauna, with particular reference to a number of commonly-occurring mite species, of the mor profile of a hemlock-yellow birch forest floor at Imp Lake, Michigan. This work, which was carried out concurrently with laboratory studies on feeding behavior (Wallwork 1958), was part of an investigation into the general biology of these forest soil mites in relation to the selective decomposition of litter and the formation of humus material. The work was supervised by Professor S. A. Graham of the School of Natural Resources, University of Michigan, and his assistance during all phases of the work is greatly appreciated. I am very grateful to the Horace H. Rackham School of Graduate Studies, University of Michigan for grants-in-aid; to Dr. E. W. Baker of the U.S. National Museum for his help with identifications; and to Drs. W. Belfield and D. J. Thomas of the University College of Ghana and Mr. J. Hobart of the University College of North Wales for helpful suggestions in the preparation of the manuscript.

THE LOCALITY

The sampling locality was the forest floor beneath a remnant of virgin forest consisting of eastern hemlock (*Tsuga canadensis* L.) and yellow birch (*Betula lutea* Michx.), with hemlock predominating. This forest stand was 30 metres wide and extended along the southern bank of Imp Lake. The soil profile showed poor to moderate development, and was of a granular mor type with fairly distinct litter, humus, and mineral layers. Raw humus, which here is considered as an intermediate stage in litter decomposition to humus, formed a separate layer in only a few places, and for the most part occurred in admixture with the litter proper. The litter layer, 2-5 cm thick, was composed of hemlock needles in varying stages of decay, except on partly covered blowdowns where moss and lichen came in. The thickness of humus varied between 2 cm and 15 cm, with an average of 4.5 cm. The mineral layer below the humus was weakly podsolised.

---

[1] Present address: Zoology Department, University College of Ghana.

Temperature readings were taken at the times of sampling in the air immediately above the forest floor, in litter at a depth of 2 cm, in humus at a depth of 6 cm, and in mineral soil at a depth of 9 cm. The mean values in these strata in summer (June to September) were: 20.3°C, 18.4°C, 16.6°C, and 15.5°C, respectively. In December the means were: −4°C, 0°C, 2°C, and 3°C, respectively.

Ground vegetation was sparse, consisting only of a few seedlings of hemlock and yellow birch, Solomon's seal (*Polygonatum* sp.), and occasional clumps of *Dryopteris spinulosa* (Muell), together with some unidentified moss, and a species of lichen of the genus *Parmelia*. This lack of ground vegetation obviated the complicating factors of faunal-floral associations to a large extent. Furthermore, this stand had no recent fire history or records of extensive disturbance to the forest floor. For these reasons the locality was suitable for studying the natural distribution and population dynamics of the animals living therein.

Materials and Methods

Samples of the forest floor were taken in adjacent pairs through the summers of 1955 and 1956, and during the winters of 1955-56 and 1956-57, from 6 samples plots, each 1 metre square, 5 metres apart on a transect through the stand. Small samples of litter, humus, and mineral layers were taken in the random manner advocated by Dice (1952) and Macfadyen (1952). These had a volume of 15.7 cc and were removed in a sampler 7 cm long, sufficient to penetrate litter and humus layers, and to enter the mineral soil in most cases. Samples were transported to the laboratory in polyethylene bags, sealed to prevent as much moisture loss as possible.

Mites were extracted from these samples immediately on arrival at the laboratory by a heating method, details of which have been published elsewhere (Wallwork 1957). Mites were collected alive in water, and were then either removed to culture cells for further observation, or mounted in Hoyer's solution (Baker and Wharton 1952) for microscopic examination and identification.

Results

Population Size

Estimates of population size have been calculated for comparison with those of other workers, although the difficulty of taking completely random samples renders these only very approximate estimates. The comparisons are shown in Table I, the figures for the present study being based on counts from about 350 samples, each 2 sq. cm in area, and with a volume of 15.7 cm^3, taken over a 2-year period. The summer estimates are from samples taken from June to September; those for winter are from samples taken in December and February. Valid comparisons of the estimates given in columns 4 and 5 of Table I cannot be made because of the wide variety of sampling techniques and extraction methods used. Murphy (1955) has pointed out that population size based on numbers per unit area or volume can give a misleading impression of the faunal characteristics of a habitat. Nevertheless the figures do give some idea of the size of populations of mites and collembola in mor profiles.

Vertical Distribution

In the summer of 1956, 150 samples of litter, humus, and mineral layer were taken; during the following winter 50 such samples were taken. Counts of mites and collembola from all 3 layers were recorded and the average values, representing numbers per 5 cm^3 are shown in Table II. The following points are noted from the Table:

(1) During the summer the numbers of mites were approximately 4 times as great as those of the collembola in all 3 layers.

(2) Mites occurred in the largest numbers in litter in summer (*i.e.* in the top 2-3 cm).

(3) The number of mites in the mineral layer was relatively small in summer and winter.

(4) The relative numbers of mites in litter and humus changed from summer to winter.

(5) The litter population showed a slight decrease in winter, whereas the humus population was more than double that for the summer.

The patterns of vertical distribution of mites and collembola at each of the 6 sample plots dur-

TABLE I. Estimates of population size of soil arthropods compared (Data from Murphy (1955) except for Wallwork's results)

Author	Habitat	Fauna	Numbers per cm.^{3}	Numbers per m.^{2}
Bornebusch (1930)	Spruce mor	Mites and Collembola	0.08	—
Ulrich (1933)	Beech-oak mull	Mites and Collembola	1.84	—
	Spruce mor	Mites and Collembola	2.12	—
Forsslund (1948)	Spruce mor	Mites and Collembola	14.6	—
Salt *et al.* (1948)	Grassland mull	Total soil arthropods	1.15	340,500
Evans (1950)	Spruce plantation	Total soil arthropods	2.42	154,600
van der Drift (1951)	Beech mor	Mites and Collembola	8.61	—
Macfadyen (1952)	Fenland	Mites and Collembola	3.18	159,400
Murphy (1953a)	Heathland mor	Total soil arthropods	2.89	834,500
Wallwork	Hemlock mor	Mites and Collembola in summer	3.24	219,200
		Mites alone in summer	2.35	176,200
		Mites alone in winter	3.95	410,500

TABLE II. Vertical distribution of mites and collembola

Stratum	MEAN NUMBERS PER SAMPLE			
	Summer		Winter	
	Mites	Collembola	Mites	Collembola
Litter	18.9	4.7	16.3	9.5
Humus	14.7	3.4	32.9	33.6
Mineral layer	1.6	0.5	0.2	0.1

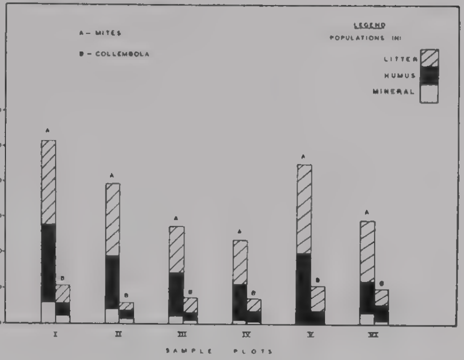


FIG. 1. Vertical disribution of mites and collembola at 6 sample plots in the summer of 1956.

ing the summer of 1956 are compared in Figure 1. During this period 35 samples, each 15.7 cm^3 in volume, were taken from each plot, and the mites and collembola from litter, humus, and mineral fractions were counted. At plot V a thick humus layer prevented sampling of the mineral layer, and only counts from litter and humus were recorded from this plot.

Figure 1 shows that the relative numbers of mites in litter and humus did not change appreciably from plot to plot. There was a greater difference between overall totals from plot to plot. At plots I, II, and V, litter and humus layers were fairly well developed and supported comparatively large populations of mites. Plots III and IV were exposed to the effects of winds and surface runoff of rainwater. These effects prevented the accumulation of litter at these plots, and consequently the humus layer was poorly developed, and the populations of mites in both litter and humus were lower than those at the other plots. Plot VI differed somewhat in profile characteristics from the others. This plot lay at one end of the transect near the border of the hemlock-yellow birch stand, in a brief transition zone between this and a stand of sugar maple (*Acer saccharum* Marshall). Here granular mor humus, typical of the hemlock-yellow birch forest floor, was giving way to a coarse mull in many places. The litter population of mites was almost twice as large as that in humus at this plot, and it is possible that a greater intermixing of mineral soil and organic matter may have affected in some way population size and distribution in the profile.

The vertical arrangement of mites and collembola in the soil profile was not permanently fixed. Changes took place in litter and humus populations throughout the year, and these may have been influenced not only by the emergence of new forms and the death of old ones, but also by the movements of animals from one layer to another. The effect of these factors will now be considered in more detail.

Population Changes

The changes in populations of mites in litter and humus were studied at sample plot 1, from analyses of 60 samples taken during various periods of the year. In Figure 2 population curves for adults and immature (juvenile) Oribatei are shown, and in this graph the separate counts from litter and humus have been combined. Population changes occurring separately in litter and humus are shown in Figures 3 and 4, and here curves for adult Oribatei, juvenile Oribatei, predatory mites, and collembola have been plotted.

Figure 2 shows that adults were more numerous than juveniles in summer, but their numbers decreased through the winter. This decrease was particularly marked in litter in winter, and this may have been due in part to a movement down

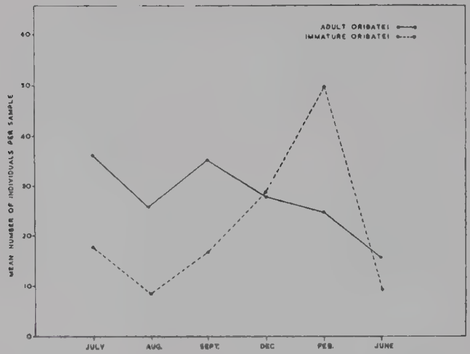


FIG. 2. Population changes in adult and immature Oribatei (litter and humus counts combined).

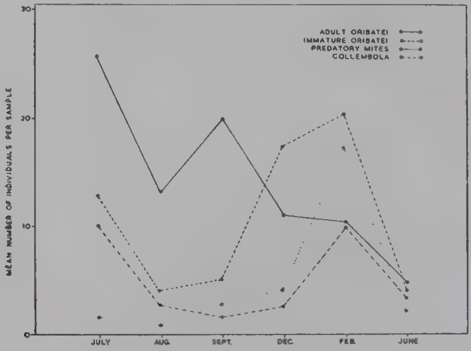


FIG. 3. Population changes in adult Oribatei, immature Oribatei, predatory mites, and collembola in litter.

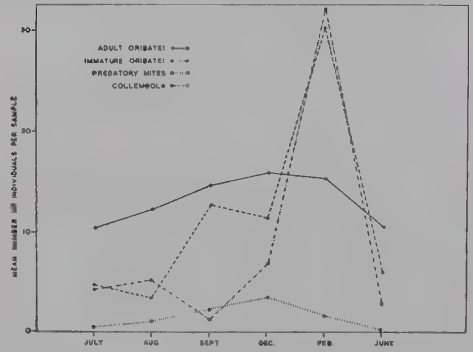


FIG. 4. Population changes in adult Oribatei, immature Oribatei, predatory mites, and collembola in humus.

into humus, where numbers of adult Oribatei continued to rise slowly until late winter, when they dropped quite sharply (Figs. 3 and 4).

The number of juveniles was relatively small during the summer, but increased markedly in winter (Fig. 2). Haarløv (1942) made a similar observation in his investigations of the soil fauna in Greenland. The ability of juvenile Oribatei to withstand frozen conditions in the soil profile has been noted by Sengsbuch (1951), and in the present study it was demonstrated by the fact that a large percentage of them occurred in litter which was completely frozen for the greater part of the winter. A large reduction occurred among juvenile forms in late winter (Fig. 2), and was probably caused by increased mortality and the change from juvenile to adult. One of the factors which may have been partly responsible for the death of juveniles in late winter was predation by other mites. In a series of culture experiments carried out concurrently with these field observations, the predatory activities of a number of mites were studied. The predators used were: *Veigaia mitis* (Berl.), *Gamasolaelaps* sp., *Pergamasus* sp., *Cyta latirostris* (Herm.), and *Rhagidia* sp. These captured and fed on soft-bodied juvenile Oribatei, but only rarely did they attack adults. Other factors may have produced mortality in juvenile Oribatei, and although it is not possible at present to determine whether or not predation acted as a population check, it may have been a contributing factor.

From time to time soil samples were washed thoroughly with benzene and water, and during this process small eggs were recovered. No satisfactory scheme for the identification of mite eggs has yet been devised, and for this reason it was impossible to divide the eggs recovered into specific categories. Oviposition was observed on a number of occasions in mite cultures, and it is fairly certain that the majority of eggs recovered from soil samples were laid by soil-inhabiting Oribatei. Egg counts during the summer showed that the number of eggs in humus was almost 3 times that in litter. The decrease in the number of adult Oribatei in litter in early August and late summer may have been partly due to a movement into humus, where eggs were laid (Figs. 3 and 4). Most of these eggs must have hatched out during the late summer or early winter, for the number of eggs in humus was very low, and the number of juveniles increased in humus, in winter. Some of the emerging juveniles may have moved upwards into litter as shown by the curves in Figures 3 and 4. Others may have completed their development to adults in humus, and remained there.

Collembolan population changes have been included in Figures 3 and 4 for they can be compared with those of the mites. Collembola were never as numerous as mites. Their numbers were low in summer, but increased remarkably in humus in winter. In this respect they followed closely the pattern of juvenile Oribatei mites, and this was particularly true of litter populations. Such features, together with the fact that these soft-bodied collembola suffered in the same way as juvenile Oribatei from the attacks of predatory mites, suggests that these collembolan populations may have been affected by some of the factors influencing population size of juvenile Oribatei.

The changes in numbers of commonly-occurring Oribatei species in litter and humus from summer to winter are shown in Table III. Here the average number of individuals in 5 cm^3 of soil sample are given. Samples were taken throughout July, August, and September, and during December.

TABLE III. Changes in populations of several commonly-occurring species from summer to early winter

Species	MEAN NUMBER PER SAMPLE			
	July/Aug./Sept.		December	
	Litter	Humus	Litter	Humus
ADULTS				
Oppia neerlandica (Oudms.)	2.2	3.9	1.0	5.0
Scheloribates pallidulus (Koch)	0.9	0.9	0.4	1.4
Tectocepheus velatus (Mich.)	0.3	0.4	0.4	0.8
Eniochthonius sp.	0.7	0.5	1.2	1.2
Phthiracarus borealis (Trgdh.)	0.7	0.4	0.9	2.0
Achipteria coleoptrata L.	1.2	0.4	0.4	0.4
Fuscozetes fuscipes (Koch)	0.3	0.2	0.05	0.2
Peloribates sp.	0.3	0.4	0.2	0.4
Mesoplophora pulchra (Selln.)	0.4	0.3	0	0
JUVENILES				
Achipteria coleoptrata L.	0.9	0.4	1.2	0.6
Fuscozetes fuscipes (Koch)	0.7	0.7	0.2	0.2

In summer 134 samples were analysed; during December the number was 50.

Changes in litter and humus populations of the species listed can be interpreted in terms of death of some adults, the movement through the profile of others, and the development to adulthood of some juveniles. The effect of these 3 factors may now be considered in relation to population changes in litter and humus at the beginning of winter, when only the litter was frozen.

Oppia neerlandica (Oudms.) was the commonest species in this locality, having the highest frequency and highest density in both litter and humus (the frequency was calculated by dividing the number of samples in which the species was present, by the total number of samples in a given series). Adults reached their peak in numbers in December in humus and at that time accounted for as much as 30% of the total adult Oribatei in this layer. Counts showed that they contributed almost 50% of the humus population of adults in July. Many adults were succesfully maintained in cultures, and proved to be active forms.

Scheloribates pallidulus (Koch) was another active form, ranging through litter and humus during summer in search of fungal hyphae which formed a large part of the food (Wallwork 1958). Adults increased in numbers in humus during winter, and there was a corresponding drop in numbers in litter.

Adults of *Eniochthonius* sp. increased appreciably in numbers in litter and humus in December. They formed about 7% of the total adult population of Oribatei in these two layers at this time. From the figures shown in Table III it is not possible to deduce whether or not directional movement up or down the soil profile took place at the beginning of winter.

Toward the end of summer counts for adults of *Tectocepheus velatus* (Mich.) were relatively low, and these indicated that some individuals probably died at this time. Numbers increased however in both litter and humus in December.

During the summer months adults of *Phthiracarus borealis* (Trgdh.) were found much more frequently and in greater density in litter samples than in humus. In winter the numbers increased in both layers, the increase being particularly marked in humus, where adults of this species formed about 12% of the total adult Oribatid fauna.

Adults and nymphs of *Achipteria coleoptrata* L. were found more commonly in litter than in humus during summer. At the beginning of winter there was a reduction in the number of adults in litter, and although the number of nymphs increased at this time, the majority of these remained in litter. A large number of larvae resembling larvae of *A. coleoptrata* bred out in culture were found in litter, and made a considerable contribution to the December peak of juveniles in this layer. Although the identification of these larvae has to be confirmed by further breeding experiments, it is clear that juveniles were more abundant than adults in this locality at this time.

Nymphs of *Fuscozetes fuscipes* (Koch) were more common than adults during summer and early winter. Counts showed that the number of juveniles increased slightly in humus in late summer, but these decreased in both layers in December.

Little change occurred in adult populations of an unidentified species of *Peloribates* from summer to winter in litter or humus. There was a slight decrease in numbers in litter at the beginning of winter, but this was probably a minor change. The larval form was identified and was very common in humus in December.

Recognisable stages of *Mesoplophora pulchra* (Selln.) were absent from litter and humus in winter. A large number of exoskeletons of adults were found in humus in winter. Adults were more common in litter than in humus during the summer, and the counts showed that there was a decrease in the number of adults in litter at the end of summer, although there was no corresponding increase in humus.

Discussion

The mite and collembolan populations of the hemlock mor were mainly restricted to a narrow zone of the soil profile which extended to a depth of 7-10 cm below the surface. Below this zone the mineral layer was coarse and sandy, containing very little organic matter. The few mites found in the mineral layer were juveniles which had probably strayed down from the humus.

The onset of winter brought about numerical and structural changes in the mite populations of litter and humus layers. These changes may be illustrated by the reactions of the species listed in Table III:

GROUP I: *O. neerlandica* and *S. pallidus*

The decrease in litter population of these adults and the increase in the humus population, at the beginning of winter, may have resulted from (1) a movement from litter to humus, or (2) the death of adults in litter, and an increase in numbers in humus caused by juveniles becoming adults in this layer. Movement may not have been solely responsible for these changes, although these were active forms and a considerable amount of downward movement may have taken place at the beginning of winter.

GROUP II: *T. velatus, Eniochthonius* sp., and *P. borealis*

The increase in the numbers of these adults in both litter and humus at the beginning of winter was probably due to nymphs becoming adults. This increase was greater than the mortality in adults. No directional movements up or down the profile could be detected at this time, and if they occurred they were masked by the increase in numbers. In this group the adult was probably the main overwintering form.

GROUP III: *A. coleoptrata, F. fuscipes, Peloribates* sp., and *M. pulchra*

In the first 3 species of this group there is no evidence that any movement down into humus occurred at the beginning of winter. The decrease in numbers in litter was probably due to mortality factors. *M. pulchra* may have moved down into humus, but this movement probably took place before the onset of winter and adults moving down into humus must have died shortly after arrival. The adult was probably not the main overwintering form in this group. The number of juveniles of some species increased quite considerably in winter (Figure 2), but in many cases identifications could not be made. The nymphal form of *A. coleoptrata* was identified. This increased in numbers in winter and may have been the main overwintering from of this species.

Using the figures in Table III, the reactions can be evaluated as follows. There was a net decrease in the litter population of about 36% at the onset of winter. The mortality in this layer at this time, expressed as a percentage of the summer population, was at least 23% (this being a minimum estimate for the mortality in Group III). A movement of individuals from litter to humus at the beginning of winter was responsible for a decrease in the litter population of 24% at the most (as represented by population changes in Group I). This was offset by an increase of about 11% in adults of species in Group II in the litter, at the beginning of winter.

The adult population in humus in December increased by about 54% of its summer value. Movement of adults of species in Group I from litter to humus at the onset of winter contributed a maximum of 22% of this increase. Juveniles becoming adults of species in Group II were responsible for about 36% increase. Mortality in humus at the beginning of winter (represented by population changes of species in Group III) was very low, being of the order of 4%.

The quantitative analysis presented above applies only to the species listed in Table III. These species represent only a small part of the forest floor community and as such are not necessarily indicators of general trends within the community. Their reactions reveal, to some extent, the complicated way in which death, the emergence of new forms, and movements through the profile, are interwoven, although it is realised that the numerical values given to these factors in the above analysis are only approximations.

Summary

1) The distribution and population dynamics of Oribatid mites and collembola were investigated in litter, humus, and mineral layers of a hemlock-yellow birch mor.

2) The greater part of the fauna was found in the top 7-10 cm of the profile which was made up of 2 distinct layers: litter and humus.

3) During summer the number of mites was approximately four times as great as that of collembola in all 3 layers, and at this time slightly more than 50% of the mite population occurred in litter.

4) In winter a decrease in numbers occurred in litter, but the humus population was more than double that in the summer.

5) In litter the largest population of adults occurred in summer, while the peak for juveniles was in winter. In humus the population of adults continued to rise slowly through summer and winter until late winter, when there was a sharp decrease. In this layer there was a marked increase in juvenile mites and in collembola in winter.

6) Population changes of several commonly-occurring Oribatid mites are discussed in relation to 3 factors: (1) death (2) emergence of new forms, and (3) movements through the profile. The effect of these factors on population changes taking place at the onset of winter are examined. Adults of some species apparently moved down into humus as the litter became frozen; others did not re-distribute themselves in the profile, but survived and increased in numbers in both litter and humus; a third group showed a reduction in numbers of adults with no increase in humus population.

REFERENCES

Baker, E. W. and G. T. Wharton. 1952. An Introduction to Acarology. New York, Macmillan.

Bellinger, P. F. 1954. Studies on soil fauna with special reference to the Collembola. Connecticut Agric. Exper. Sta. Bull. 583.

Birch, L. C. and D. P. Clark. 1953. Forest soil as an ecological community with special reference to the fauna. Quart. Rev. Biol. **28**: 13-36.

Bornebusch, C. H. 1930. The Fauna of Forest Soil. Forstl. Forsøgsv. Danm. **11**: 1-224.

Dice, L. R. 1952. Natural Communities. Ann Arbor, University of Michigan Press.

Eaton, T. H. and R. F. Chandler. 1942. The fauna of forest humus layers in New York. Cornell Univ. Agric. Exp. Sta. Mem. **247**: 1-26.

Evans, G. O. 1951. Investigation on the fauna of forest humus layers. Forestry Commission; Report on forest research for the year ending March 1950. London, H. M. Stationery Office. 110-113.

Fenton, G. R. 1947. The soil fauna: with special reference to the ecosystem of forest soil. J. Anim. Ecol. **16**: 76-93.

Forsslund, K. H. 1948. Något om insamlingsmetodiken vid markfaunaundersökningar. Medd. Skogsforskn. Inst., Stockh. **37, (7)** 1-22.

Haarløv, N. 1942. A morphologic-systematic-ecological investigation of Acarina. Medd. om Grønland **128**: 1.

Hairston, N. G. and G. W. Byers. 1954. The soil arthropods of a field in southern Michigan; a study in community ecology. Contrib. Lab. of Vert. Biol. University of Michigan **64**.

Jacot, A. P. 1936. Soil structure and soil biology. Ecology **17**: 359-379.

———. 1939. Reduction of spruce and fir litter by minute animals. J. Forestry **37**: 858-860.

———. 1940. The fauna of the soil. Quart. Rev. Biol. **15**: 28-58.

Macfadyen, A. 1952. The small arthropods of a *Molinia* fen. J. Anim. Ecol. **21**: 87-117.

Murphy, P. W. 1953a. The biology of forest soils with special reference to the mesofauna or meiofauna. J. Soil Sci. **4**: 155-193.

———. 1955. The ecology of the fauna of forest soils. In Soil Zoology: London, Kevan, Butterworths.

Pearse, A. S. 1946. Observations on the microfauna of Duke forest. Ecol. Mongr. **16**: 127-150.

Salt, G., F. S. Hollick, F. Raw, and M. V. Brian. 1948. The Arthropod population of pasture soil. J. Anim. Ecol. **17**: 139-152.

Sengsbuch, H. G. 1951. Notes on some New York Oribatid mites. Zoologica **36**: 3.

Tragardh, I. 1929. Studies on the fauna of the soil in Swedish forests. Inter. Congr. Ent., Ithaca, **1928**: 2.

Ulrich, A. T. 1933. Die Makrofauna der Waldstreu. Quantitative Untersuchungen in Beständen mit guter und schlechter Zersetzung des Bestandesabfalles. Mitt. Forstwirt. Forstwiss. **4**: 283-323.

van der Drift, J. 1951. Analysis of the animal community in a Beech forest floor. Tijdschr. Ent. **94**: 1-168.

Wallwork, J. A. 1957. The Acarina of a Hemlock-Yellow Birch forest floor. Thesis, University of Michigan.

———. 1958. Notes on the feeding behavior of some forest soil mites. Oikos **9**: 260-271.

Weis-Fogh, T. 1948. Ecological investigations on mites and Collemboles in the soil. Natura Jutlandica **1**: 139-270.

ECOLOGY OF THE CHUB, *GILA ATRARIA,* WITH SPECIAL EMPHASIS ON VERTEBRAL CURVATURES, IN TWO OCEAN LAKE, TETON NATIONAL PARK, WYOMING[1]

Kenneth R. John
Franklin and Marshall College, Lancaster, Pa.

Introduction

Two Ocean Lake, which was annexed to Teton National Park in 1950, was reported by long-time residents of the area and by the Wyoming Game and Fish Commission to have experienced a tremendous increase in chub which followed a sharp decline in trout, *Salmo clarki lewisi.* During the rise of the chub, residents of the area made a concerted effort to annihilate the great blue heron, *Ardea herodias*. It was also reported that the lake contained an unusually high frequency of deformed chub (curvatures of the vertebral axis). Under the protection of the National Park Service and a proposed restoration of the lake, a rise in trout and heron, two of the main predators of the chub, might be expected. This suggested an opportunity for a study of predation in nature with special reference to predation on deformed chub.

Field studies, carried out in the summers of 1956 and 1957, were directed toward an evaluation of the problem—basically a study of the ecology and life history of the chub with special interest in the question of whether or not it would be possible in future years to detect and attribute a decrease in deformed chub to the anticipated increase in predators. This would require estimates of the annual abundance of deformed chub, which would require a knowledge of their distribution in the lake relative to that of the normal chub. Aside from statistical applications, information on the distribution might have a bearing on the question of the causes of the deformity. Is the cause environmental, hereditary, or some combination of the two? Also, comparative rates of survival of normal and deformed chub under existing low predation should be determined. Finally, a comparison of the frequency of deformities in the Two Ocean Lake population with that in other populations should be made to aid in determining whether or not the Two Ocean Lake situation is unique, as has been reported.

I think it is important to mention in passing that the field work and laboratory experiments sought to answer these questions, and did yield a valuable backlog of information. But many aspects remain insufficiently known to report.

This paper presents findings on (1) the limnology of the lakes (2) the ecology and life history of the chub (3) the frequency of deformed chub in different lakes, and (4) the distribution of chub in Two Ocean Lake. The results are derived primarily from Two Ocean Lake, and secondarily from Emma Matilda, Ox Bow, and Enos lakes. All of the lakes are in the Snake River drainage.

Materials and Methods

Temperatures of the water were measured with a Whitney thermistor thermometer, and quantities of dissolved oxygen were determined by the Winkler method.

In Two Ocean Lake, fish were collected from deeper waters in traps and from shallow waters with a seine. In other lakes, seines were used in shallow waters and gill nets in deeper waters. Traps (patterned after fyke nets) were 4 feet square and 8 feet long with a single, one-funneled entrance. Neither leads nor bait were used. In anticipation of small fish, the trap used in 1956 was made with plastic window screening (3 mm sq. mesh). In 1957 traps were made with ½-inch (stretched measure) 6-20 cotton seine stock. The seine (½-inch stretched measure) was 6 feet deep and 100 feet long without a bag. Gill nets were 6 feet deep and composed of 50-foot sections of 1½, 2½, 2, 3, and 4-inch mesh (stretched measure).

Traps were set on the bottom in water 2 to 3 meters deep and were attended about 20 hours later, having fished over-night. Seining was done during the day except for 1 sample collected at night.

Estimates of the age composition of normal chub in the samples were obtained by determining the ages, by the scale method, on a subsample and then applying the age-length indices obtained from the subsamples to the total samples for which fork-lengths had been recorded. Ages on all deformed chub from these samples were determined from scales. Estimates of the sex ratios and of the proportions of sexually mature fish in each

---

[1] This work was supported by a grant from the National Science Foundation through the Jackson Hole Biological Research Station of the University of Wyoming and the New York Zoological Society. I wish to acknowledge the very able assistance of Ross M. Horrall in 1956 and of Irvin Lawrence in 1957.

age group were based on analysis of subsamples.

In 1956 (John 1957) all chub were tabulated under individual age groups, but in the present paper all chub from age groups VI and older are grouped in the single age-category, VI and over. (An error occurs in the paper of 1957: Scales were misread and all fish should be one year older than reported.) Chub collected in seines during the day are grouped in the age-category II. These fish were almost entirely of age groups I and II.

Qualitative analysis of the stomach contents of the chub were made periodically at Two Ocean Lake, and also on the occasions of sampling other lakes. The stomach contents of trout were also examined.

At stations 1 and 5, in 1956, chub were marked by cutting off one pectoral fin, and were released at the sites of capture.

A sample is defined as a single catch in any of the types of fishing gear. Young chub means age groups I and II; older chub are age groups III and above.

Limnology and Sampling Stations

Two Ocean Lake

Two Ocean Lake, shown in surface profile in Figure 1, is vaguely divided into an eastern basin with a maximum depth of 9 meters, and a western basin with a maximum depth of 21 meters. Around most of the lake, the depth increases rapidly from the shoreline. In the western basin, the 5-meter depth contour, which is roughly the limit of rooted vegetation, is within 15 meters of the shore, except in the western-most end where it lies between 60 and 100 meters off shore. In the eastern basin, the 5-meter contour is near the shore around the northern side of the lake, but from the northeastern corner continuously to station 5, the 5-meter contour lies between 50 and 150 meters off shore. Most areas within the 5-meter contour support luxuriant beds of *Ceratophyllum demersum,* and lesser amounts of *Myriophyllum exalbescens.* In shallower waters, *Sagittaria acuneata, Potomageton pictinatus* and *P. richardsonii* become more abundant.

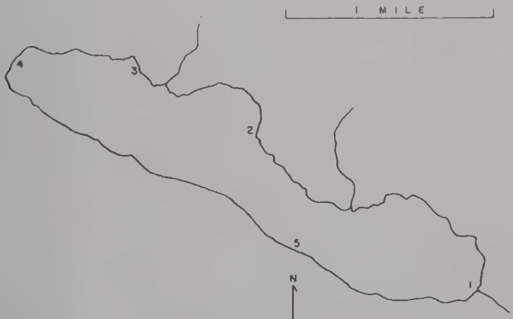


FIG. 1. Surface profile of Two Ocean Lake, showing sampling stations.

Affluent streams occur at station 4, east of station 3, and east of station 2. The effluent stream is located at station 1. After the spring flood stage, the rate of flow in the stream at station 4 is inconsequential; the stream east of station 3 stops flowing; and the stream east of station 2 flows at a rate of about ¼ c.f.s. Generally by early August, depending on the seasonal precipitation, the effluent stream stops flowing.

Representative profiles of temperatures and dissolved oxygen are shown in Table I. From the middle of June onward, there is insufficient oxygen below a depth of 7 meters to support fish. During these studies, the highest surface temperature recorded was 20.9° C. At a depth of 1½ meters, the temperature never exceeded 19.5° C.

TABLE I. Distributions of temperatures and dissolved oxygen in Two Ocean Lake

	6-12-57		6-28-56		8-6-56	
Depth Meters	Temp. C°	Dissolved Oxygen ppm	Temp. C°	Dissolved Oxygen ppm	Temp. C°	Dissolved Oxygen ppm
0	14.6	7.8	19.0	8.0	19.3	—
1	14.6	—	18.5	—	19.2	8.2
2	14.6	8.1	17.3	—	19.1	—
3	12.8	8.7	16.6	—	19.1	—
4	8.6	8.7	15.5	8.5	19.1	—
5	6.4	7.4	10.2	7.8	18.5	8.1
6	5.8	—	7.5	5.9	12.4	6.2
7	5.4	—	6.9	1.9	9.9	—
8	5.0	—	6.0	0.8	8.8	0.5
9	5.0	—	5.8	—	7.7	—
10	4.8	0.2	5.5	0.2	7.1	0.5
11	4.8	—	5.3	—	6.7	—
12	4.8	—	5.2	—	6.3	—
13	4.8	—	5.1	—	6.1	—
14	4.6	—	5.0	—	5.9	—
15	4.6	—	4.95	—	5.7	—
16	4.4	—	4.8	—	5.6	—
17	4.2	0.04	4.75	—	5.5	—
18	4.4	—	4.7	—	5.4	
19	4.4	—	4.6	0.0	5.3	—
20	4.4	—	4.5	—	5.1	
21	—	—	—	—	5.1	—

Hills surrounding the lake protect it from the prevailing winds. Rarely does the surface become choppy and there is little vertical transport of water as is evident from the profiles of temperatures. Distributions of temperatures and dissolved oxygen have not been studied in the winter. Whether or not spring and autumnal overturns occur is not known.

In 1956, chub were collected at stations 1 and 5; in 1957, at stations 1, 2, 3, 4, and 5. Stations were established where traps could be used. Stations 2 and 3 were limited in extent because the bottom sloped abruptly into deep water at a distance of 20 meters from shore. Rooted vegetation occurred largely on the slope. Station 1 extended along the eastern end between the north and south shores. Station 4 extended along the entire western end, and station 5 extended about 200 meters east from the number 5 shown in Figure 1. Stations 1, 4, and 5 were comparatively similar. The bottom sloped gradually into deeper water and was heavily colonized with rooted vegetation.

Other Lakes

Emma Matilda, which lies parallel and about ¾ of a mile southward, is very similar to Two Ocean Lake in shape and dimensions. It has a smaller drainage basin, no affluent streams, and is isolated from Two Ocean Lake except when the effluent stream flows during early spring, and then the two lakes are connected only through their common drainage, Pacific Creek. Rooted vegetation is sparsely distributed.

Ox Bow is a former channel of the Snake River and is still broadly connected with the river. It lies about 1½ miles below the dam on Jackson Lake. As an average, it is about 6 feet deep and supports an abundance of rooted vegetation, predominantly *C. demersum,* and *M. exalbescens.*

Enos Lake lies about 15 miles northeast of Two Ocean Lake, and at a higher elevation. The drainage basin is large and the effluent stream is permanent. The alga, *Chara* sp., covers the bottom from a depth of ⅓ meter to 3 or 4 meters. *Charex* spp. form dense stands in shallow water.

CHUB, LIFE HISTORY

In 1956, the first sample, July 1, contained ripe males, a few ripe females, and many females which had not ovulated. In 1957, the first sample, June 18, contained numerous ripe males, but none of the females had ovulated. The first ripe females were caught on July 3. Large numbers of spawning chub were caught daily through July 22 after which date field operations were temporarily suspended. In the first half of August, a small number of spawning chub were caught. Although spawning activities were intense for about 3 weeks in 1957, the greatest activity spanned a 5-day period centering on July 9. During these 5 days, from sunrise until about 0800 hours, small schools of chub were seen spawning near shore in water less than ½ meter deep. Although the exact limitations of spawning sites are not known, spawning seems to occur profusely over all vegetated areas, and most of the eggs are shed in areas where the water exceeds 1 meter in depth.

In the laboratory, at a constant temperature of 18.2° C, the eggs hatch within 9 days; and at 19.6° C, they hatch within 6 days. The duration of incubation in the lake is not known, but probably lies between 6 and 15 days for most eggs according to the distribution of temperatures during the spawning period in the areas of maximum spawning. Eggs located in shallow water near shore may be subjected to slightly higher temperatures during the day and hatch in less than 6 days.

Additional life-history information is embodied in the length-frequency histogram, Figure 2, of the combined samples of 1957. The histogram derives its odd shape—decrease in frequencies for lengths under 166-175 mm.—from the behavior of the chub. Spawning chub are attracted to the traps judging from the fact that traps are ineffective after the spawning season and from the fact that most of the trapped chub were sexually mature. Note in Table II that the traps yielded only 104 fish of age group II and none of age group I although the traps would retain either of these age groups. This accounts for the near absence of fish below the interval 106-115. Note also in Table II that the proportions of fish increase stepwise through age group III and reach a peak in age group IV.

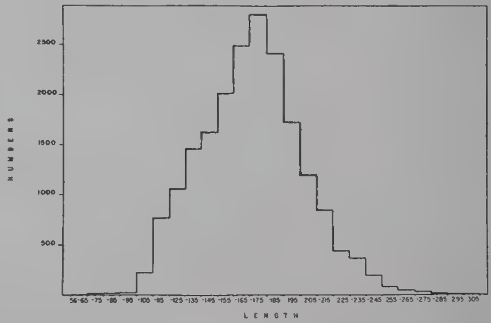


FIG. 2. Length-frequency distribution of combined samples from traps for all stations in 1957. Total number of fish equals that of Table 2. Lengths plotted in 10 mm. class intervals.

TABLE II. Age composition of combined samples from traps for all stations in 1957

Age Group	II	III	IV	V	VI & over
Number of Specimens......	104	3967	5654	5080	5701

The distribution of sexes and maturity, Table III, based on subsamples from the traps in 1956, indicates that age group III is totally immature and that one might expect less than 15% maturity in age group IV and still incomplete maturity in age group V. If spawning fish are attracted to the traps and if, in turn, immature fish are attracted to spawning groups, but not to the traps, one would expect a misrepresentation of age groups III, IV, and V in the traps. Age group III would probably be most misrepresented because its members grade in size into age group II and could be expected to segregate from larger fish as is true of age groups I and II. This does not necessarily mean that age group III aggregates with age groups I and II. A point of additional interest lies in the evidence of Table III that sexually maturity is not simply a function of age, but also of size. Additional data would be needed to establish this point.

TABLE III. Distribution of sexes and maturity in 2 subsamples of chub from traps in 1956

Age	MALE		FEMALE		Per Cent Mature
	Mature	Immature	Mature	Immature	Both Sexes
3	0	34	0	26	0
4	4	24	2	16	13
5	4	1	8	3	75
6	13	0	6	0	100

The decrease in frequencies of chub in class intervals below 166-175, in the histogram, may result partly from fluctuations in abundance of year classes. But this matter must be interpreted cautiously because the distribution of age groups in the lake is not uniform, and an apparent fluctuation in the abundance of year classes could be caused by non-representative samples (see results on distribution).

The decrease in age group V, Table II, and in the frequencies for class intervals beyond 166-175 seems to mark the beginning of the mortality curve. Most chub over 180 mm fork-length belong to age groups VI and over. This portion of the histogram is thought correctly to represent the population. Mortality rates rise rapidly in age group VI. The maximum longevity is not known; 8-year old chub were uncommon, and 9-year old chub were rare.

ECOLOGY

Food

Stomach contents of the chub were examined especially to learn of the extent to which they feed on fishes. In the course of the two summers, remains of minnows (Cyprinidae) were found in 2 chub from Two Ocean Lake, and in 2 from Emma Matilda Lake. All 4 of these chub exceeded a fork-lentgh of 320 mm. However, the stomachs of other large chub contained no fish. The food habits change with age. The youngest chub feed entirely on zooplankton and other invertebrates. The diet continues to be mainly zooplankton in chub less than 170 mm long. Chub larger than this are omnivorous, feeding extensively on the young branches of *Ceratophyllum* and *Myriophyllum*. These feeding habits seem to hold true for Two Ocean, Emma Matilda, and Ox Bow lakes. In Enos Lake, the entire digestive tract of all chub examined was distended with *Chara*.

Other Fishes in Two Ocean Lake

In 1956, the collection contained the following numbers: *Catostomus fecundus*, 587; *Pantosteus platyrhynchus*, 2; *Richardsonius balteatus hydrophlox*, 6632; and *Rhinichthys osculus carringtonii*, 28. A few hybrids between *Rhinichthys* and *Richardsonius* were caught at station 4.

In 1957, the following numbers were collected: *C. f.*, 137; *P. p.*, 2; *R. b. h.*, 2242; *R. o. c.*, 7; and *Salmo clarki lewisi*, 1. After July 10, samples contained large numbers of *Richardsonius*, but the fishes in these samples were not enumerated.

The following information was obtained from the Wyoming Game and Fish Commission. In 1948, a gill net, 40 feet long, composed of 1-inch (stretched measure) mesh collected 90 *Gila* and 1 *Salmo c. l.* from a set in 1 meter of water near the outlet. In 1952, 12 samples were collected with gill nets from various parts of the lake. Each net consisted of 25-foot sections of the following mesh sizes (stretched measure): 1½, 2, 2½, 3, 3½, 4, 4½, and 5-inch. The samples contained 31 *Salmo c. l.*, 2 *Salvelinus fontinalis*, 1180 *Gila*, and 407 *C. f.* Ten of the *Salmo* weighed as an average 0.54 lbs each; the average weight of the others was somewhat less than 3 lbs.

Predators

At Two Ocean Lake, the stomachs of most larger trout (2 to 7 lbs) caught by sportsmen, contained 1 to 4 *Gila* with occasional specimens of *Richardsonius*. Trout under this size were not commonly caught, and the stomachs of those examined contained invertebrates. Stomachs were examined on 18 trout in 1956, and 21 trout in 1957. All *Gila* taken from the stomachs were normal. In Enos Lake, trout stomachs contained no evidence of fish.

Great blue heron from a rookery on Ox Bow Lake fished at Two Ocean Lake every day, there being usually 4 to 6 present at one time and occasionally as many as 10. In 1956 and again in 1957, approximately 80 American mergansers, *Mergus merganser*, were reared at the lake. Two or 3 white pelicans, *Pelecanus erythrorhynchos*, were on the lake on most days. Other piscivorous birds were rare. A small heron rookery exists on Enos Lake.

Parasites and Diseases

At Two Ocean Lake, in June and July of 1956, and to a lesser extent in 1957, chub with acute fungal infections could be seen in any part of the lake. These sick chub were probably more abundant than deformed chub, and certainly were less capable swimmers.

All of the chub in Two Ocean Lake were heavily infected with various nematodes, and about 1 in 100 with the large larval tapeworms, but they seemed to be largely insensitive to their parasites.

ABUNDANCE OF DEFORMED CHUB

At Two Ocean Lake, in 1956, 145 (1.07%) of 13, 543 chub from traps were deformed. In 1957, 173 (0.52%) of 32,896 were deformed. These collections represent samples in which an exact count was made, but not all of these samples were processed for age-composition estimates. It is assumed that most of the chub were over 2 years old.

The percentages of deformities at different stations are given in Table IV. Excepting station 1, the lowest percentages were obtained at stations that had not been fished in 1956—stations 2 and 3. However, station 4 had not been fished in 1956 either, and it yielded a higher percentage of deformities.

TABLE IV. Total samples and percentages of deformed chub from traps at different stations. Numbers here do not equal those in Table II. Some of these samples were not processed for age determinations. Includes only a few fish less than 3 years old

Station	1956		1957	
	Total Samples	% Deformed	Total Samples	% Deformed
1	7700	0.98	14000	0.48
2	—	—	6896	0.31
3	—	—	3145	0.54
4	—	—	7328	0.76
5	5706	1.22	1700	0.77

At station 1 in 1956, the normal chub were returned alive to the lake, but only 24 of 75 deformed chub were returned; 51 were killed and preserved. At other stations in 1956, and in 1957, discriminatory killing of deformed chub was not practiced; the entire samples were either returned or destroyed.

TABLE V. Total samples and percentages of deformed chub collected by seine. These fish are predominantly of age groups I and II

Station	1956		1957	
	Total Samples	% Deformed	Total Samples	% Deformed
1	5494	0.54	10939	0.77
2	—	—	1210	0.91

Percentages of deformities in the age-category II are given in Table V. Unfortunately, it was not possible to seine at other stations nor to find concentrations of younger chub near these stations at sites that might have been seined. Deformities in younger chub were about half as frequent as in older chub in 1956, and about as frequent as in older chub in 1957.

At Emma Matilda, there were no deformities in 646 older chub, nor in 300 chub of age group O. At Ox Bow, there were no deformities in 543 older chub. At Enos, there were no deformities in 626 older chub, nor in 300 younger chub. There was one deformity in a sample of 1514 chub of age group O.

DISTRIBUTION IN TWO OCEAN LAKE

During the day, older chub are not frequently seen in waters less than 3 meters deep. Chub in age groups I and II press into the shoreline in concentrations often containing 5,000 to 10,000 individuals. Others in these age groups are scattered throughout the vegetated areas. Chub in age group O, at least to the end of August, do not appear in concentrations, but rather are scattered more or less uniformly throughout the vegetation within the 1-meter contour. At stations 1, 4, and 5 one could observe large numbers of chub, and could readily locate deformed chub from a boat.

In the evenings, beginning just before dark, the larger chub were very active at the surface, apparently feeding, and extended shoreward into the 1-meter depth zone. Judging from seining results (effort would be a better term) young chub apparently moved out beyond the 1-meter depth during the night. After dark, schools of older chub could be observed briefly by turning on a light as the boat drifted quietly. Only the eastern basin was surveyed at night. The activity at the surface was evident everywhere, but it seemed most concentrated within the 2- to 5-meter depths.

Marked chub were recaptured predominantly at the stations of their original capture and release, but the numbers recaptured were small. Of the 3,721 chub marked, 39 were recaptured in 1956, and 20, in 1957.

Age composition estimates of normal chub for different stations are shown in the histograms of Figure 3. Although the results for each station were different, two patterns seem prominent. At stations 2 and 3, abundance increases stepwise with age, while at stations 1, 4, and 5, younger fish predominate.

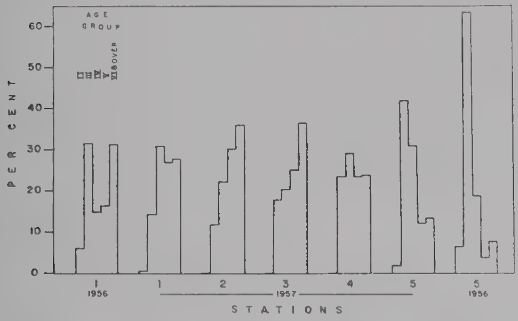
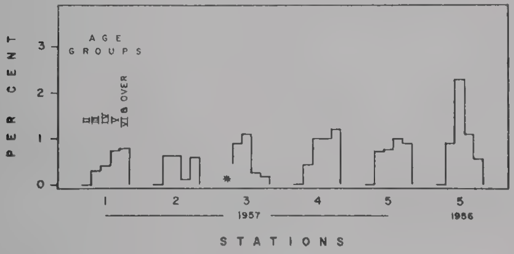


Fig. 3. Age composition of combined samples from traps for each station. Numbers of fish represented are as follows: 1956, sta. 1, 783; sta. 5, 2384; 1957, sta. 1, 6883; sta. 2, 2849; sta. 3, 3128; sta. 4, 5964; sta. 5, 1687.

Percentages of deformed chub by age groups for the different stations are given in Figure 4. The values for all age groups fall within the expected range of variation for small numbers (assume 1% deformed).



*One of 20 (5%) in age group II was deformed.

Fig. 4. Percentages of deformities in each age group for each station. Numbers of deformed fish were as follows: 1956, sta. 5, 25; 1957, sta. 1, 41; sta. 2, 13; sta. 3, 17; sta. 4, 55; sta. 5, 13. Data not available for station 1, 1956.

Discussion

Percentage Deformed

In 1956 (John *op. cit.*) the samples from stations 1 and 5, treated statistically, could be considered as representing the same population. The estimate of 1.1% deformed chub for the entire lake seemed reasonable. In 1957, the average percentage deformed (0.52) was a significant decrease from 1956, but the cause of this decrease was not determined. There is no reason to think that it was caused by predation. It could have resulted from collection methods, or it could be a sampling error.

This decrease could have resulted from the discriminatory killing of deformed chub at station 1 in 1956, if, as was suggested in the records on the distribution of marked specimens, the chub tend to be territorial. The decrease at station 1, alone, was significant, and it weighed heavily on the average for the lake because 14,000 of the total collection came from station 1.

On the other hand, the decrease in 1957 could mean that natural mortalities of older deformed chub exceeded recruitment from age group II. The results suggest that in 1956, deformed chub of age group II were about half as frequent as they were in the older age groups. Proportionately, the percentages of deformities in older chub at station 5 exceeded those from station 1 by about the same amount in 1957 as in 1956. Perhaps this means that the recruitment did not equal the mortality, and it implies that the proportion of deformities in age group II was the same in all parts of the lake. It is interesting that station 4, with a habitat very smililar to 1 and 5, but, like station 5, not subjected to discriminatory killing of deformed chub in 1956, produced the same value of deformities as station 5 in 1957. But this is subjective evidence because station 5 was not adequately sampled in 1957.

Although stations 2 and 3 were not sampled in 1956, the low percentages of deformities caught there in 1957 possibly do portray a consistent annual pattern. Assuming that the causes of the low percentage of deformities at station 1 have been correctly limited, stations 2 and 3 produced fewer deformities than any of the other stations, and because 10,903 chub were collected there, the results weigh heavily on the average for the lake.

It seems probable that the estimate for 1956, lacking samples from stations 2 and 3, was too high; and the estimate for 1957, being heavily weighted by the results from station 1, was too low. The real value of deformities for the entire lake for both years probably lay between 0.5% and 1.0%.

One wonders what proportion of the eggs in a given year produce deformed chub. Is the percentage of deformities that hatch, or at least that survive, likely to be the same in all parts of the lake? An affirmative answer was implied in comparing stations 1, 4, and 5, but it cannot be proven because the causes of the deformities are not known. If they are the product of environmental factors such as high temperatures or oxygen deficiencies, as reported for other fishes by Price (1940) and Stockard (1921), the numbers produced in different parts of the lake might differ, if the conditions differ. No effort was made to study microhabitats. On the other hand, the numbers of deformities produced might be genetically determined as has been reported for other fishes by Aida (1930) and Rosenthal and Rosenthal (1950) and Rosenthal *et al.* (1958). As such, the numbers would be largely independent of evironmental conditions. The question remains unanswered, but it would not be surprising to find uniform percentages of deformities produced at different stations because, in the laboratory, at constant temperatures and with adequate oxygen, the average numbers of deformed offspring from different combinations of parents (normal and deformed) were apparently equal. These results on offspring will be reported elsewhere.

It was hoped that estimates of the percentages of deformities in each age group at different stations would clarify this question of whether or not deformities are uniformly distributed, and that they might indicate whether or not there is a differential survival of normal and deformed chub as was suspected in 1956 (John *op. cit.*), but the samples of each age group were too small. In order to find out what role chance has played in the results, on numbers that differ by say. 0.25%, one would need about 10,000 chub of each age group from each station. This would mean collecting and measuring a minimum of 300,000. In fact, because age groups are not equally abundant, nor equally captured, the total collection would be much larger. It would be impractical to attempt such studies. Two men expended over 150 hours in collecting, measuring, and estimating ages on 21,000 chub, and this was not a collecting problem—the average size of the sample was around 4,000 chub.

At a level of 1%, the deformities are certainly less frequent than was intimated in early reports. Various explanations might be offered, but I think the early reports were exaggerated. Yet, low as this value is, deformities seem to be unusually frequent for a natural population in what appears to be a typical lake except possibly with regard to the history of its predators. Certainly there are fewer deformed chub in Enos Lake, perhaps also in the other lakes studied. The literature on vertebral deformities in fishes is, indeed, extensive, but most articles deal with anatomical descriptions. I was unable to find estimates on the abundance of such deformities for possible elucidation of the Two Ocean Lake situation except for the work of Sigalas (1925) on *Atherines presbyter,* where the author was unable to account for the high frequency; the work of Meen (1952) on the Arctic char in Chubb Crater Lake, Canada, in which the deformities were attributed to malnutrition (which would be an improbable explanation for Two Ocean Lake); and the study by Hubbs (1959) on *Gambusia affinis* in isolated warm springs. According to Miller (pers. comm., 1958), hot springs often harbor fishes with a high frequency of vertebral deformities. Otherwise, if one excludes data from fish-culture stations, accounts in the literature imply that the deformities are rare.

Distribution of Normal Chub

Generalizations on the distribution of chub in the lake must be made reservedly because samples were collected only during the spawning season, they were not collected simultaneously from all stations, some of them are inadequate in size, and very little weight can be given to the data on the distribution of marked chub.

Perhaps younger chub are localized and older chub, especially spawners, have as their territory the entire lake. It would seem particularly true that age groups, O, I, and II, are localized, and their location is probably fixed as the place of hatching. Stations 1, 4, and 5, were the sites of the most intense spawning and were also characterized by a preponderance of young chub, and this included age groups III and IV. Stations 2 and 3 appear to have very small permanent populations and are populated diurnally by migrating older chub. Whether or not the same chub return to these stations each night is not known. Older chub could travel the length of the lake within a day, but how much they do move in contrast with their ability to move is not known.

It is clear that samples collected only at one station can be misleading. It is also clear that stations with a particular kind of habitat produce similar, though perhaps distinctive, samples.

Predators

Predators are not abundant at Two Ocean Lake. Whether or not any of the predatory species will increase under the management of the National Park Service is not known, but it is unlikely that the trout will increase because they have no dependable spawning sites, immigration is negligible if not nonexistent, and the lake is open to fishing as of 1956. Perhaps the chub prey on young trout which would also minimize the importance of trout as predators on chub. Jordan and Evermann (1896) state that chub are destructive of young trout. But this is currently not important in Two Ocean Lake, because young trout are rare. Unless chub show a high preference for trout, their role as trout predators is unimportant because, in these studies, they were rarely piscivorous.

It is possible that newly-hatched chub are preyed upon by older chub, especially age groups I and II, and by the shiner, *Richardsonius,* because these fishes occupy the same habitats as the newly-hatched chub. Food habits of fishes might be studied profitably during the hatching season of the chub. These are the only fishes (if predatory) of sufficient abundance to play a possible role in selective reduction of deformed chub. It is otherwise inconceivable that deformed chub at their present low frequency, would be reduced by selective predation, because with the high abundance of normal chub, chance would seem to favor the survival of deformed chub, under effective predation.

Predator-prey interactions may be simple, involving highly specific food habits of the predators, but probably most commonly, as discussed by Allee *et al.* (1949), are quite complex, involving a variety of non-specific predators and a number of different species of prey. The effectiveness of predators in reducing a species of prey commonly varies proportionately with the density of the prey. After one species of prey, which might be called the favored one, is reduced to a low level, the predators take an increasing toll of secondary prey. Predators can be considered effective when they can reduce the population of prey by feeding on its normal members. They can be considered marginal if they can only capture the sick, crippled, or otherwise weakened individuals. Trout in Two Ocean Lake are not sufficiently understood to be classified as effective or marginal predators on the chub. As was mentioned, chub taken from trout stomachs were normal, but they could have been diseased and thus easy prey.

The piscivorous birds may increase under National Park Service protection, and they may reduce the chub population, but it seems unlikely that they would select deformed chub because they require more food than this and they catch normal fish effectively. Their fishing habits appear to be independent of the swimming ability of the fishes.

SUMMARY

Chub begin spawning around July 1, and continue into August, but most spawning is done in about 3 weeks in July. Eggs probably hatch in 6 to 15 days. Sexual maturity is apparently a function of size as well as of age. Natural mortality rates rise abruptly in chub over 5 years old. Longevity is unknown, but 9-year old chub were rare. Younger chub are predominantly insectivores and planktonivores and become more herbivorous with age.

Reliable estimates of the age composition of the population and of the percentages of deformities were difficult to obtain because the behavior of the chub is not well known. Younger chub are apparently territorial and older chub disperse, but still show some tendency to be territorial. Approximately 1% of the chub have deformities of the vertebral axis. Although this value is numerically low, it seems to be high for natural populations not subjected to obvious teratogenic mechanisms such as high temperatures. Still, the value is too low to make a study of predation practical.

Predators of the chub, chiefly mergansers, great blue heron, and cutthroat trout are not abundant. Birds may increase under the protection of the National Park Service, but trout will not become important under existing conditions of open fishing.

REFERENCES

Aida, T. 1930. Further genetical studies of *Aplocheilus latipes.* Genetics **15**: 1-16.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. *Principles of animal ecology.* Philadelphia and London, W. B. Saunders.

Hubbs, C. 1959. High incidence of vertebral deformities in two natural populations of fishes inhabiting warm springs. Ecology **40**: 154-155.

John, K. R. 1957. Comparative rates of survival of normal and deformed chub, *Gila atraria* Girard, in Two Ocean Lake, Teton County, Wyoming. Proc. Penna. Acad. Soc. **31**: 77-82.

Jordan, D. S. and B. W. Evermann. 1896. Fishes of North and Middle America. Bull. U. S. Nat. Mus. No. 47.

Meen, V. B. 1952. Solving the riddle of Chubb Crater. Nat. Geog. Mag. **150**: 1-32.

Price, J. W. 1940. Time-temperature relations in the incubation of the white-fish, *Coregonus clupeaformis* (Mitchell). Jour. Gen. Physiol. **23**: 449-468.

Rosenthal, H. L., P. R. Myers, and M. K. Bruning. 1958. Spinal curvature, a mutation in the swordtail, *Xiphophorus.* Jour. Hered. **49**: 238-242.

Rosenthal, H. L. and R. S. Rosenthal. 1950. Lordosis, a mutation in the guppy, *Lebistes reticulatus.* Jour. Hered. **41**: 217-218.

Sigalas, R. 1925. Frequence des deformations du squelette chez l'Atherine. Actes. Soc. Linn. Bordeaux. 77 Proc. Verb.: 173-174.

Stockard, C. R. 1921. Developmental rate and structural expression: an experimental study of twins, 'double monsters' and single deformities, and the interaction among embryonic organs during their origin and development. Am. J. Anat. **28**: 115-266.

STUDIES ON THE BIOLOGIES OF TWO MITE SPECIES, PREDATOR AND PREY, INCLUDING SOME EFFECTS OF GAMMA RADIATION ON SELECTED DEVELOPMENTAL STAGES

Charles J. Rohde[1]
Health Physics Division, Oak Ridge National Laboratory,[2] Oak Ridge, Tennessee

Introduction

Among the many organisms forming a part of the soil ecosystem, mites are conspicuous in both numbers of species and individuals. Studies of soil fauna indicate that, through the breakdown of organic matter by digestion, these small arthropods are important agents in promoting soil fertility (Kubiena 1955). One of the interests of this laboratory is in the ground disposal of radioactive wastes and in the resultant effects upon soil dwelling and soil forming organisms (Auerbach 1958). Data have been obtained concerning the effects of radiation on the mixed species of mites in a community. These data are highly complex and their proper analysis and interpretation requires detailed knowledge of radiation effects at the single-species level.

The present study is concerned with the biologies of two mites species, *Caloglyphus mycophagus* (Megnin 1874) (Sarcoptiformes: Acaridae) and *Fuscuropoda marginata* (C. L. Koch 1839) (Mesostigmata: Uropodidae) including the gross effects of gamma radiation on selected developmental stages.

The author is deeply indebted to such members of the Health Physics Division as Dr. Stanley I. Auerbach, Dr. Joseph H. Camin (Consultant), and Dr. Orlando Park (Consultant) for assistance during the course of the investigation and to Mr. E. G. Struxness for making the study possible. Thanks are due Dr. Marvin E. Kastenbaum of the Statistics Section, Mathematics Panel, Oak Ridge National Laboratory. Mr. Albert L. Broseghini of Iowa State College helped with much of the work while a temporary summer employee. Particular thanks are due Dr. Joseph H. Camin, Chicago Academy of Sciences, for the identification of *Fuscuropoda marginata* and to Dr. H. H. J. Nesbitt of Carleton University, Ottawa, Ontario, Canada for the identification of *Caloglyphus mycophagus*.

Materials and Methods

In order to utilize mites as experimental animals, it was necessary to select species that would be adaptable to laboratory procedures and to develop special rearing techniques and equipment. Berlesates from soil, litter and organic debris yielded a large oribatid fauna available for culture purposes, but studies of the life histories of galumnid (Sengbusch 1954) and phthiracarid mites (Rohde 1955) indicated that these might have life cycles requiring up to two months for completion. Examination of chicken litter, an additional habitat that is rich in organic matter, revealed large numbers of *Caloglyphus mycophagus*. This mite is easily reared in the laboratory and produces a large number of eggs during its short life span. Obtained from the same source was *Fuscuropoda marginata*. This species was not reared successfully in the laboratory until it was discovered by the writer to be a predator of *Caloglyphus*.

Cultures were developed for both species under consideration, utilizing small plastic boxes containing a water-holding layer composed of plaster of Paris and activated charcoal.

Examinaion of berlesates from chicken litter revealed that the *Caloglyphus* mites were feeding upon the dead bodies of lepidopterous and dipterous larvae. Later, the use of ground beef as food proved equally successful. Mold growths frequently appeared when a rearing technique employing a humid atmosphere was used. The hyphae not only interfered with close observation, but the growth entrapped the immature mites. Prior to the isolation of eggs, a food consisting of pulverized lepidopterous larvae soaked in a 10,000-unit suspension of Mycostatin, a fungistatic compound marketed by E. R. Squibb and Company, was placed to one side of the rearing chamber. At this concentration there is no apparent effect upon the mite. Additional drops of the suspension were added during an extended period of observation.

In the studies on *C. mycophagus*, several pairs of mites and sufficient food were placed in separate chambers formed of plastic cylinders imbedded in a plaster-charcoal mass contained in a plastic sandwich box (Rohde 1956). These are illustrated in Figure 1. The mites were removed to a new chamber at regular intervals and in this manner a record of egg age could be kept. In the

---

[1] Present address: Department of Biology, Northern Illinois University, DeKalb, Illinois.

[2] Operated by Union Carbide Nuclear Corporation for the United States Atomic Energy Commission.

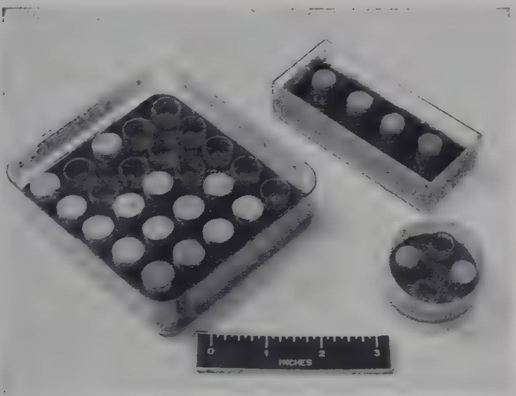


FIG. 1. Types of plaster-charcoal rearing boxes used in these studies. From left to right these are: (1) Sandwich box containing 25 chambers for life history studies, (2) Plastic box for general culture purposes, (3) Round containers for use in C_0^{60} facility, (4) Individual lucite cylinder which serves as the mite chamber.

life history study and in the selection of virgin material, single eggs were removed to rearing chambers with a fine brush and placed upon the bare plaster-charcoal substrate. Although a relatively small amount of food was placed in each chamber, the larva was occasionally hidden from view. In these instances, it was possible to determine its existence without disturbing the food by noting the presence of the empty egg case.

The life history study was made over a period of 11 days. At the start, eggs of known age (about 2 hours) were isolated in ten 25-chamber rearing boxes and kept in a constant temperature cabinet at 25° C. Water was added to the charcoal substrate of each box on 3 occasions during the 11-day period in order to maintain a high humidity in the boxes. Examinations of the chambers were made at 4-hour intervals throughout the period of observation. Observations required the removal of the cork stopper with the examination being made by means of the stereo-microscope. Lengths of stadia, periods of inactivity between stadia, and the removal of exuviae following ecdyses were recorded.

Laboratory cultures of the predator, *Fuscuropda marginata,* were maintained by daily introduction into the rearing boxes of 100 or more of the acarid prey plus food for the acarids. Because of the habit of the female *F. marginata* of inserting eggs in the food of the prey, it was necessary to dissect out most of the eggs used in radiation experiments. Eggs of *F. marginata* were collected daily from mass cultures and placed in the chambers of radiation boxes with a fine brush.

The collection of *Caloglyphus* eggs for irradiation purposes was accomplished by placing 3 to 5 pairs of mites, along with small amounts of food, into each of 4 chambers, where they were allowed to reside for a period of 24 hours. Then the adults were removed and the eggs were subjected to gamma radiation. By means of this routine the maximum egg age at the time of irradiation was 24 hours. Successive egg clutches were subjected to increasingly larger radiation exposures at air dose rates of 19 r/sec. The delivered doses ranged from 250 to 3,750 r. At the expiration of a 5-day waiting period, hatched larvae were killed with a few drops of boiling water and counts of larvae and unhatched eggs were made. Virgin adults of both species were similarly exposed to a range of gamma doses. These were mated with normal individuals and counts were made on the hatchability of the eggs produced.

Radiation boxes for experiments with *Fuscuropoda* and *Caloglyphus* were made from round plastic containers (Fig. 1). These containers were 1¾ inches in diameter and one inch in height. The diameter was the maximum size which could be inserted in the Cobalt^{60} radiation chamber.

RESULTS

Biology of Caloglyphus Mycophagus

Members of the Acaridae are widely distributed in a variety of habitats where they feed upon organic derived from numerous sources. Included are dead animals, farinaceous products, rotting plant material, wastes in the nests of birds and mammals (Nesbitt 1945) and cheese. The caloglyphids are known saprophages feeding chiefly upon dead and decaying insects.

The sexes are not difficult to distinguish; the presence of copulatory suckers flanking the anus identifies the male. Copulation between virgin adults occurs within seconds following pairing. The male locates the female, crawls about her body and takes up a final position behind her, facing in the opposite direction. The caudal end of the male is superimposed upon that of the female. The pair may remain an hour or less in this position with copulation apparently occurring intermittently during this period of time.

The eggs, which begin to appear within 12-15 hours of continuous pairing, are deposited on the food, the substrate, the wall of the rearing chamber or on the cork stopper. The egg is oval, translucent, and without ornamentation. The daily egg laying record (Figure 2) shows that the largest number of eggs are produced during the first 4 days of pairing and that production decreases to zero after 2 weeks. It can also be seen

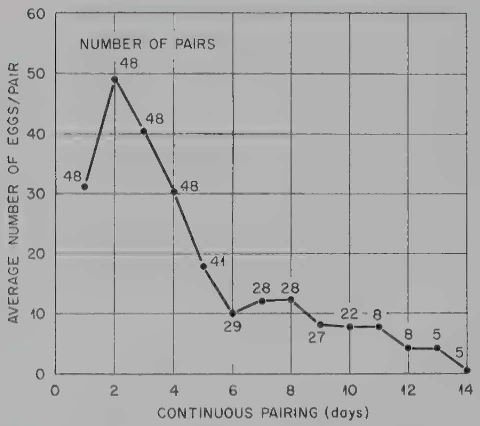


FIG. 2. Daily egg laying record from virgin stock of *Caloglyphus*. Average number of eggs per pair per day is indicated.

that the mortality rate of the adults rises after the fifth day and greatly increases after the tenth day. Using virgin adults, egg production from 26 pairs was recorded every 6 hours for a 10-day period. During the diel cycle no significant difference was observed, there being approximately the same number of eggs obtained during each of the six-hour periods.

Upon hatching a larva backs out of the egg case, begins to move about and thereafter is characteristically found within or on the food. After an inert period, characterized by a cessation of visible activity, ecdysis occurs and the 8-legged protonymph becomes active. The protonymph also passes through an inert period and then molts to give rise to the tritonymph. After a final inert period the tritonymph molts to the adult form. Thus, this mite passes from the egg through 3 active stadia, 3 inert stadia and 3 molts before the adult state is attained. Typically, the inert period is passed way from the food and usually upon the bare substrate in contact with the wall of the rearing chamber.

The deutonymph occurs between the protonymph and tritonymph stages only under certain conditions. This deutonymph or hypopus is a stage commonly found in the acarids. The conditions which determine the formation of the hypopus are largely unknown. During this stadium no food is taken and, with the aid of suckers on its underside, the hypopus is able to adhere to smooth surfaces. Collections of other mites, insects, birds and small mammals frequently include numbers of clinging hypopi. At no time under the conditions employed in the life history study of *Caloglyphus* did hypopus formation take place. However, in mass cultures involving a meager food supply, food chiefly of plant origin, or large numbers of predators, numerous hypopi were formed.

Life History Studies

Two hundred and fifty eggs of known age were isolated individually in the chambers of 10 rearing boxes. Examinations of the chambers were made at 4-hour intervals until a number of adults were obtained. The results of this study are summarized in Figure 3.

Of the 247 mites (98.8% hatch) considered at the outset, none passed through the incubation period in less than 9 hours and all but one completed this phase in less than 53 hours. One egg took as long as 79-83 hours to incubate. Fifty % of the eggs completed incubation in less than 41 hours. Except for one individual, the larval stadium ranged from slightly less than one day to slightly more than 4 days. Fifty % of the mites completed this stadium in less than 43 hours. Time required for the protonymph stage ranges from 9 hours to nearly 5 days. Fifty % of the total completed this period in less than 28 hours. For the tritonymph stage, the range extends from 14 hours to nearly 4 days. The median time in this stadium is about 31 hours. One hundred and fifty-eight, or approximately two-thirds of those hatching, survived to the tritonymph stadium; most of the loss was due to frequent handling, since only one dead specimen was observed.

The 3 inert periods are short; all individuals completed these stadia in less than one day. Over 85% of the total passed through each of these inert periods in fewer than 13 hours. Distribution of the times in the active stadia are skewed to the right (Fig. 3). Time required for incubation of the eggs is skewed to the left.

An approximate record, to within a 4-hour interval, was kept on the length of time between egg and adult for 158 mites. The average duration of the life cycle, as computed from these observations, was about 151 hours (6⅓ days). The shortest observed cycle was just under 4 days while the longest was slightly more than 9 days.

Biology of Fuscuropoda Marginata

Members of the Uropodidae are of no known medical or economic importance. Many are frequently found attached to insects during a nymphal stage by anal pedicels. However, this is merely a means of dispersal and, prior to the present study, none were thought to be predaceous in habit (J. H. Camin *in litt.*). It was not possible to carry

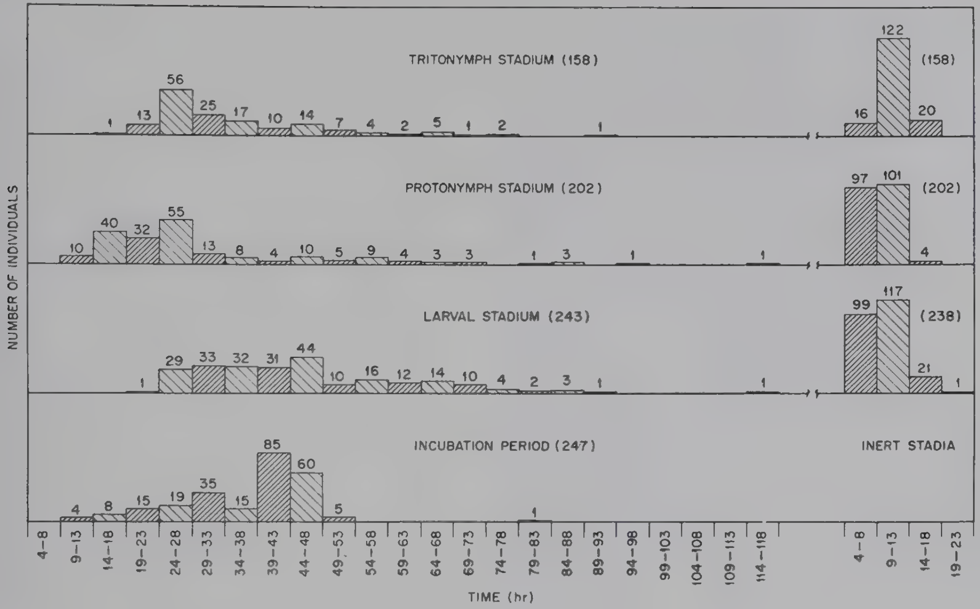


FIG. 3. Summary of developmental stadia in *Caloglyphus.*

out a detailed investigation on the length of the life cycle but continued observation suggested a range of 30-40 days.

The newly emerged female copulates immediately. Copulation in *Fuscuropoda marginata* was observed on a number of occasions. In fact, one or more males may gather around a female still in the process of shedding the last nymphal skin. During copulation both sexes face in the same direction with their ventral surfaces opposed. A round, transparent ball, the spermatophore, appears in a position between their opposed genital openings. It was not possible to keep this under continued surveillance; however, the spermatophore appears to be crushed rather than punctured and at the end of a 10-minute period, the pair separate. Subsequent examination of the female revealed the remains of the ball as a whitish, triangular sheet with the apex directed anteriorly and conforming to the general outline of the epigynial shield.

Occasionally, eggs are found free on the plaster-charcoal surface but usually they are partially inserted in some detritus such as acarid remains. A longer incubation period is required for the eggs of *Fuscuropoda* (Table I), than for those of *Caloglyphus.*

Large numbers of *F. marginata* were found in the same habitat with *Caloglyphus.* These were placed in small rearing boxes with some litter for food. Frequent observations during a 10-day period revealed that no feeding was taking place. No *Fuscuropoda* eggs appeared until after a number of *Caloglyphus* were introduced into the culture. Later examination showed only the sclerotized remains of the acarid mites.

TABLE I. Incubation time for eggs of *Fuscuropoda marginata*

Days	Number Hatched
4	2
5	1
6	19
7	48
8	4
9	1
11	1

Additional acarids were introduced into the culture dishes to test the circumstantial evidence of predation. Within a short period of time the *Fuscuropoda* began to attack the *Caloglyphus.* Subsequently, the act of contact, attack and feeding by this uropodine predator was observed (Figure 4) many times. *Fuscuropoda* entraps the prey by using its palpi and first pair of legs. At the same time its exserted chelicerae move swiftly over the body surface of the prey. The act usually begins with cheliceral contact on the dorsal surface, but actual penetration invariably occurs through the ventral surface and most frequently in the area between legs I-II on either side of the body. During what appears to be a search for

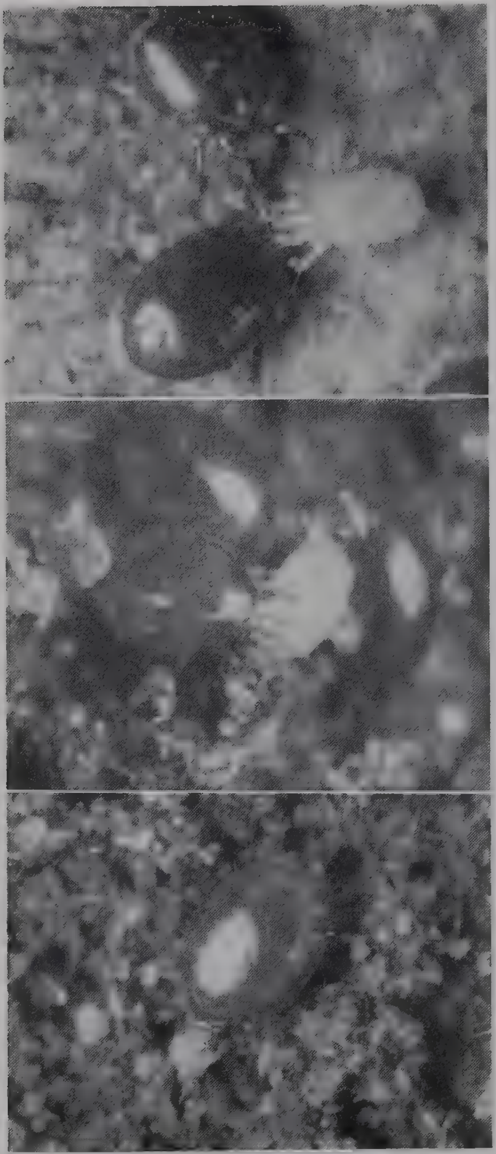


Fig. 4. Predation of *Caloglyphus* by *Fuscuropoda* showing contact, attack and remains of the prey.

a point of entry, the chelicerae may be extended for a distance of about one-half the body length. Penetration is accomplished by exerting a push with the chelicerae held together as a spear. When the body fluid of the prey is exuded, the attacker stops and employs a rapid posterior-anterior movement of its chelicerae driving the fluid toward its mouth. However, the chelicerae are more frequently moved about within the body of the acarid and used as a pliers in tearing apart the internal organs. Tearing action stops periodically and cheliceral movements serve to scoop out the food and direct it toward the mouth. As feeding continues and the viscera are consumed, the acarid eventually becomes a shapeless mass recognizable only by its sclerotized legs and mouthparts.

Caloglyphus has no apparent means of protection and all stages, with the exception of the egg, are subject to attack. However, the hypopus stage appears least acceptable for food, although it is not completely overlooked and occasionally one can be seen in the process of being devoured. During one experiment, approximately 250 acarid mites were consumed by 19 *F. marginata* adults in 7 hours. At another time the same number devoured more than 300 of the prey in 4 hours. That this voracious mite will attack other soft-bodied animals was observed in chicken litter berlesates, when 6 adults were found with their chelicerae inserted in a living caterpillar. *Fuscuropoda* larvae also have been observed in the act of predation on larval acarids. In culture boxes they have been observed crawling within partly consumed acarids. The nymphals stages likewise are predaceous.

Gross Effects of Gamma Radiation

A total of 5,778 *Caloglyphus* eggs of maximum 24-hour age were irradiated with instantaneous gamma doses ranging from 250 to 3,750 r. The percentage hatchability was calculated for each clutch of eggs at each dose. These effects were compared with the hatchability of 5,968 untreated eggs which served as controls (Figure 5). The LD_{50} is calculated to be 2,930 r with a standard error of approximately 75 r.

In the experiments paralleling those on *Calo-*

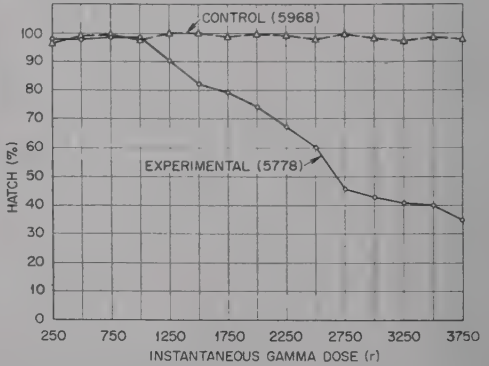


Fig. 5. Hatchability in irradiated compared with untreated *Caloglyphus* eggs.

glyphus, 188 eggs of *Fuscuropoda* of maximum 24-hours age were irradiated with gamma doses ranging from 100 to 3,000 r, averaging 18.8 eggs per dose increment. Total mortality occurred at 2,000 r. The 24-hour eggs were used, because eggs of this age were irradiated in the experiments with the eggs of *Caloglyphus.* However, *Fuscuropoda* eggs at a maximum 24-hour age have completed only about one-seventh of their development time (Table I) whereas those of *Caloglyphus* have completed about one-half their development at this time. Therefore, in another series of experiments, 447 *Fuscuropoda* eggs of 84 hours age, averaging 37.2 eggs per dose, were irradiated. Eggs of this age are at an approximate mid-point in the incubation period. Hatchability was virtually unaffected by doses up to 3,000 r (Figure 6)

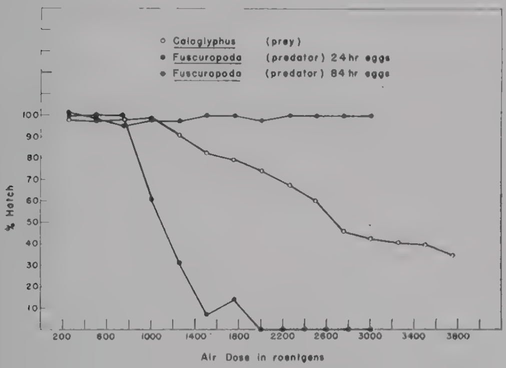


Fig. 6. Comparison of radiosensitivities between eggs of prey and predator.

Experiments involving irradiation of the adult stage were also conducted for each of the species. *Caloglyphus* males were exposed to 4,000 (6 irradiated, 5 control), 5,000 (7 irradiated, 2 control), and 8,000 r (12 irradiated, 12 control) gamma doses. These were paired with normal virgin females and a record was kept of the hatchability of the eggs produced during each 24-hour period of continuous pairing. These data are summarized in Figure 7.

At the lower doses, fertility approaches that of controls on the fifth day of post-irradiation pairing. At 8,000 r hatchability ranges from 19 to 37% of normal during the first 3 days of mating. It is during this period, under normal conditions, that egg production is highest. Fertility appears to return to normal after the eighth day of pairing, a time at which egg production is normally low and when death frequently occurs. That the return to fertility in the male is real and not a function of reduced egg production in the female was shown in a separate series of experiments. Six males, irradiated at 5,000 r, each received a normal virgin female every third day of post irradiation pairing. Results showed that sterility is temporary and that fertility returns to the male by the fifth day at this dose level.

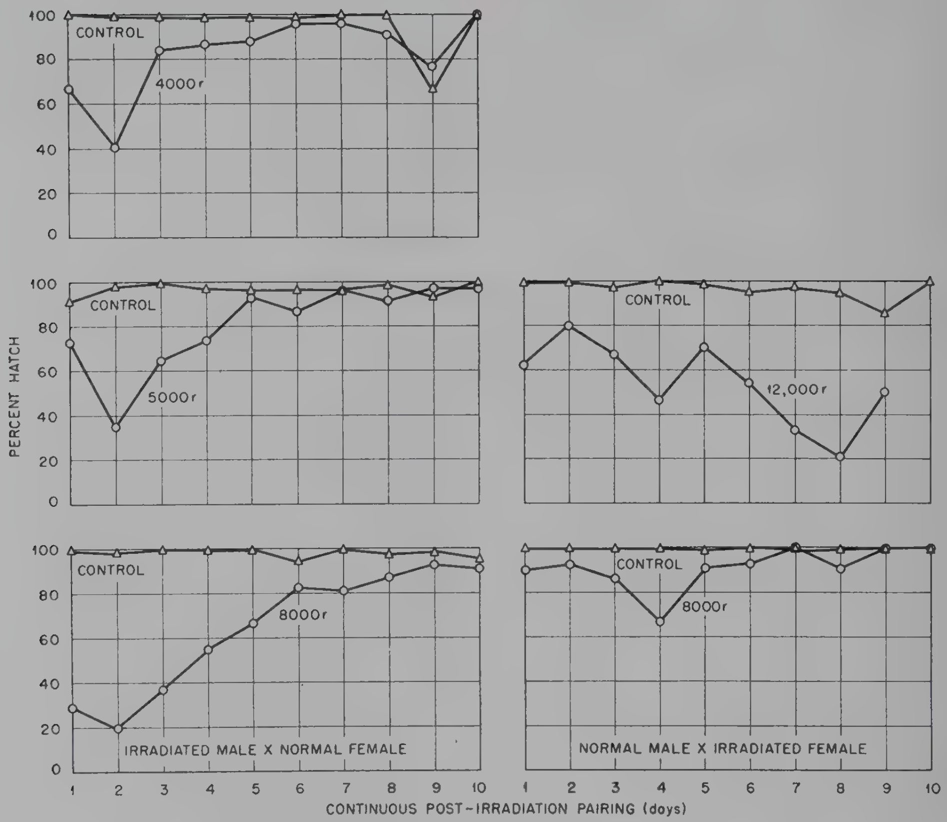
As shown in Fig. 7 the lowest hatchability occurred in the eggs produced during the second 24-hours period of continuous pairing. A separate series of rearing experiments, utilizing the progeny produced in the second egg clutch of irradiated fathers, are incomplete. Hatched larvae were isolated in a rearing chamber with a small amount of food. In over 100 such isolations 18 developed to adults. Of the remaining immature *Caloglyphus* mites, many did not survive and a few showed no obvious growth.

Virgin *Caloglyphus* females were irradiated at 8,000 (6 irradiated, 6 control) and 12,000 r (10 irradiated, 2 control) doses. These were paired with normal unmated males and a record was kept of hatchability of the eggs produced during each 24-hour period of continuous pairing. Effects of radiation upon the female are slight at 8,000 r, but are more marked at 12,000 r (Fig. 7).

In experiments similar to those on *Caloglyphus, Fuscuropoda* males were exposed to 8,000 (6 irradiated) or 15,000 r (6 irradiated) and paired with normal females. Ten untreated males served as controls. The results are summarized in Table II. A striking difference in effect is observed in *Fuscuropoda* males as compared with those of *Caloglyphus.* The toxic effect of radiation is lasting; there is no return of fertility.

Table II. Radiation-induced sterility in *Fuscuropoda marginata* males

	Dose (r) 5,000		15,000		Controls	
Day	Eggs	Hatch (%)	Eggs	Hatch (%)	Eggs	Hatch (%)
1	0	[0.0]	0		0	
2	5	0.0	3	0.0	5	100.0
3	15	20.0	5	0.0	19	94.7
4	12	25.0	20	0 0	30	100 0
5	21	9.5	16	6.2	35	82.8
6	28	7.1	14	0.0	35	97.1
7	20	10.0	14	0.0	33	93.9
8	25	4.0	14	0.0	27	88.8
9	14	14.2	14	0.0	36	97.2
10	26	3.8	10	0.0	43	97.6
11	25	8.0	12	0.0	11	90.9
12	22	0.0	11	0.0	8	87.5
13	28	3.5	7	14.2	10	80.0
14	23	8.7	9	0.0	9	77.7
15	21	0.0	8	0.0	6	50.0
16	16	0.0	7	14.2	5	100.0
17	16	0.0	8	0.0	9	77.7
18	18	0.0	12	0.0	9	100.0
19	22	0.0	15	0.0	11	90.9
20	27	0.0	10	0.0	10	100 0



Radiation-Induced Sterility in *Caloglyphus*

FIG. 7. Radiation-induced sterility in treated, paired with untreated, *Caloglyphus* mites. The 3 graphs to the left show the effect of dose on hatchability of eggs and length of sterile period in treated males. The graphs to the right show the effect of hatchability of eggs from treated females.

DISCUSSION

Most of the available information on the sterilizing effects of radiation on arthropods deals with insects. Howden (1957) summarized some of the information on mortality and sterilization produced by gamma and X-rays in certain Diptera, Hymenoptera, Orthoptera and Coleoptera.

Few radiation data dealing with mites are available from the literature or from current investigations outside of this laboratory. Rodriquez (1948), working with bean plants containing P^{32}, reported that the 2-spotted spider mites on these plants produced more offspring than did mites on the control plants.

The eggs of *Caloglyphus* and *Fuscuropoda* appear to be less sensitive to radiation than those of such arthropods as *Habrobracon* (Whiting 1945), *Melanoplus* (Tahmisian 1953) and *Drosophila* (Hassett 1952, citing Dittrich). However, comparisons are difficult to make because of the variety of material used for study by different investigators and because of the variations in sensitivity seemingly correlated with the stage of embryonic development.

Other relevant findings include the work of Yanders (1954) who noted an increase in fertility, during a 10-day observation period, in *Drosophila robusta* males exposed to 5,000 and 7,500 r X-ray doses. Similarly, a return of fertility in *Caloglyphus* males was observed. No return of fertility was obtained with the males of *Fuscuropoda*. The length of the fertile period of *Caloglyphus* males decreased linearly with increased gamma dosage. This finding agrees with the work of Gowen and Stadler (1951) involving the use of X-radiation on *Drosophila melanogaster* males. The males used in the *Caloglyphus* experiments were never more than 2 days old at the time of pairing. Bonnier and Lüning (1950) found that neither age nor the unmated state of *D. melanogaster* males seemed to have any influence on the hatchability of eggs. Bushland and Hopkins (1951) found that almost complete sterility was induced in male screwworm flies with an X-ray dose of 2,500 r, whereas no effect was observed in the similarly irradiated females. Complete sterility in *Caloglyphus* males was not found with gamma doses as high as 8,000 r. A slight effect on hatchability of eggs from females receiving the same dose was obtained.

Although the present study is preliminary in scope and dosages, particularly in the experiments with adults, are exploratory in nature, certain facts are evident. A distinct difference in radiosensitivity exists between the 2 mite species. When comparing eggs of comparable age (in amount of embryonic development), the egg of *Fuscuropoda* appears insensitive to gamma doses which obviously affect hatchability in the egg of *Caloglyphus*. On the other hand, *Caloglyphus* males are not only less sensitive to doses which produce permanent sterility in the males of *Fuscuropoda,* but they also show a return of fertility. The respective radiosensitivities in females of the 2 species remains to be determined.

The need for further investigation is evident in the lack of information on the effects of gamma radiation on nymphal stages, total life span and other aspects of the biology of these mites.

This study is concerned only with the effects of instantaneous doses of gamma radiation. Another important avenue of investigation would be to determine the effects of chronic exposure to sublethal doses of radiation on the prey, the predator and the predator-prey interrelationship.

SUMMARY

The present study is concerned with some gross effects of gamma radiation upon 2 members of the Acarina, prey and predator.

The life history of *Caloglyphus mycophagus,* the prey, is described in detail. The average duration of the life cycle was slightly more than 6 days with a range from 4 to 9 days. Observations on the life history of *Fuscuropoda marginata,* the predator, are also presented. These indicate a life cycle ranging from 30 to 40 days.

Data on the effects of radiation upon hatchability of eggs and upon viability of eggs from irradiated virgin adults are presented. *Fuscuropoda* eggs are insensitive to doses producing 50% mortality in *Caloglyphus* eggs of comparable age. The predator male is rendered permanently sterile by doses that produce temporary sterility in the prey male.

REFERENCES

Auerbach, S. I. 1958. The soil ecosystem and radioactive waste disposal to the ground. Ecology **39:** 522-529.

Bonnier, G. and K. G. Lüning. 1950. X-ray induced dominant lethals in *Drosophila melanogaster.* Hereditas **36:** 445-456.

Bushland, R. C. and D. E. Hopkins. 1951. Experiments with screw worm flies sterilized with x-rays. Jour. Econ. Ent. **44:** 725-31.

Hassett, C. C. and D. W. Jenkins. 1952. Use of fission products for insect control. Nucleonics **10:** 42-46.

Howden, H. F. 1957. Investigations on sterility and deformities of Onthophagus (Coleoptera: Scarabaeidae) induced by gamma radiation. Ann. Ent. Soc. Amer. **50:** 1-9.

Kubiena, W. L. 1955. Animal activity in soils as a decisive factor in establishment of humus forms. Soil Zoology, Butterworths Scientific Publications, London, pp. 73-82.

Nesitt, H. H. J. 1945. A revision of the family Acaridae (Tyroglyphidae), order Acari, based on comparative morphological studies. Canad. J. Res., D **23:** 139-188.

Rodriquez, J. G. 1948. The effect of a 3-month exposure of mites to radio-phosphorus. Ohio State Univ. Eng. and Expt. Sta. News **22:** 1-3.

Rohde, C. J. 1955. Studies on arthropods from a moss habitat with special emphasis on the life history of three oribatoid mites. Doctoral dissertation, Northwestern University Libraries.

———. 1956. A modification of the plaster-charcoal technique for the rearing of mites and other small arthropods. Ecology **37:** 843-44.

Sengbusch, H. G. 1954. Studies on the life history of three oribatoid mites with observations on other species. Ann. Ent. Soc. Amer. **47:** 646-667.

Tahmisian, T. N. and H. H. Vogel, Jr. 1953. Relative biological effectiveness of fast neutrons, gamma rays, x-rays on grasshopper nymph ovarioles (*Melanoplus differentialis*). Proc. Soc. Exp. Biol. and Med. **84:** 538-543.

Whiting, A. R. 1945. Effects of x-rays on hatchability and on chromosomes of *Habrobracon* eggs treated in first meiotic prophase and metaphase. Amer. Nat. **79:** 193-227.

Yanders, A. 1954. X-ray induced dominant lethals in *Drosophila robusta.* Genetics **39:** 558-64.

SINGLE-FACTOR ANALYSIS IN POPULATION DYNAMICS[1]

R. F. Morris
Forest Biology Laboratory, Fredericton, New Brunswick, Canada

Introduction

In the study of natural populations it is desirable but not always feasible to measure the effects of all mortality factors. This requires frequent population sampling, supported by data on natural enemies, climate, and other factors, and leads to the compilation of detailed life tables for successive generations. These tables must be compiled simultaneously for a number of different environments if it is desired to learn why population density varies in place as well as in time. It is important to know, for example, why a forest insect periodically develops high populations in certain well-defined stand types but not in all types where it occurs. This multi-factor approach therefore demands much time and effort and, for species that are difficult to sample, is more suitable for a team of investigators than for the individual.

A preliminary examination of rather extensive life-table data for the spruce budworm, *Choristoneura fumiferana* (Clem.), suggested that the factors affecting this species in any one place are of two types—those that cause a relatively constant mortality from year to year and contribute little to population variation, and those that cause a variable, though perhaps much smaller, mortality and appear to be largely responsible for the observed changes in population (Morris 1957). A factor of the latter type will here be called a 'key factor,' meaning simply that changes in population density from generation to generation are closely related to the degree of mortality caused by this factor, which therefore has predictive value.

This leads to some interesting questions: Do these key factors exist for other species or are most populations affected by so many interacting factors that they behave like random numbers? If a key factor is suspected in a population, can its existence be demonstrated effectively by a very limited 'single-factor' approach in which only population density and the mortality caused by this factor are measured in each generation? If so it may be possible, with the expenditure of only a few man-days each season, to discover relationships of value for the prediction of population changes. This would be particularly useful for certain species of economic importance which, because of their behavior or habitat, do not lend themselves to a more comprehensive multi-factor study.

The object of this paper is to present and discuss two examples of single-factor analysis for natural populations. The first applies to the black-headed budworm, *Acleris variana* (Fern.), a defoliator of fir and spruce; and the second to the European spruce sawfly, *Diprion hercyniae* (Htg.), a defoliator of spruce. The records to be used cover 12 generations of the budworm and 24 of the sawfly and apply to a period (1946-1958) when neither species was limited in numbers by its food supply. Parasitism in the larval stage will be used for both species to represent the suspected key factor. Population density is measured at one stage of larval development, when the important parasites are inside the host, and parasitism is measured by dissecting or rearing the larvae from this sample. Although other studies are being conducted on both species, this part of the work requires only a few days each generation.

Nicholson and Bailey Model

The analysis for the two defoliators is concerned with only two variables—population density and larval parasitism—and the object is to learn whether parasitism is a key factor in the sense that the degree of parasitism in one generation can be used to predict larval population in the next generation. It may therefore be helpful to consider first one of the simple population models that have been developed to show what might happen if population changes in any one place depended entirely upon one factor. Such a factor, in the terms used here, would be a perfect key factor. The model presented by Nicholson and Bailey (1935) will be used for this purpose because the selected single factor—parasitism—is common to both the model and the present examples of natural populations.

Let h = host population density
k = the proportion of h affected by the key factor
s = surviving host population = $h(1-k)$
n = any generation of the host
$n+1$ = the generation following n
F = the effective rate of increase of the host

---

[1] Contribution No. 501, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

from generation to generation when $k = 0$

Then if population variation from generation to generation is determined by only one factor,

$$h_{n+1} = Fh_n\,(1 - k_n) = Fs_n$$

$$\text{or, } \log h_{n+1} = \log F + \log h_n + \log\,(1 - k_n) = \log F + \log s_n$$

The conversion to common logarithms makes the equation rectilinear and has other important advantages. Changes in animal populuations are geometric, not arithmetic, and it is therefore meaningful to think in terms of log h rather than h. On this basis, an increase in density of 2 to 4 has the same magnitude as an increase of 200 to 400. Again, nearly all forest insect populations that have been studied carefully have been found to follow the negative binomial distribution (Morris 1955). Conversion to logarithms is necessary to stabilize variance and permit valid statistical analyses when different population densities are involved.

Theoretical values of log h and log s for successive generations can be calculated from the above equation, using the simplifying assumptions of Nicholson and Bailey concerning the searching behavior of parasites. That is, $\log\,(1 - k_n) = -\,ap_n/2.3$ where a, the area of discovery of the parasite, is independent of h, and p_n is adult parasite population in the n^{th} generation. An example has been plotted (Figure 1A) in which F has been assigned an arbitrary value of 4.

For reasons that will later become apparent, the relationship between $\log h_{n+1}$ and $\log h_n$ is of interest and has also been plotted (Figure 2A). A figure is formed in clockwise sequence by the points for successive generations, but this is an open figure with the points spiralling farther apart. This results from the model's assumptions about the action of parasites, which lead to oscillations of increasing magnitude. If it were understood how oscillations are damped, the model could no doubt be refined so that a closed figure would be obtained.

It is also worth while to plot $\log h_{n+1}$ over $\log s_n$ (Figure 3A), because this suggests a useful way of testing a suspected key factor in natural populations. For the model the correlation must, of course, be perfect ($r = 1$) because the possibility of other *variable* mortality is excluded as well as the possibility of sampling error in measuring both population and mortality. The regression line is represented by the equation $\log h_{n+1} = \log F + \log s_n = 0.0602 + \log s_n$. The intercept on the vertical axis is log F, where F was assigned a value of 4, while the slope (b) can have no other value than unity. The relation between $\log h_{n+1}$ and $\log s_n$ may also be seen, in a temporal sequence, by mentally moving the broken line of Figure 1A one generation to the right.

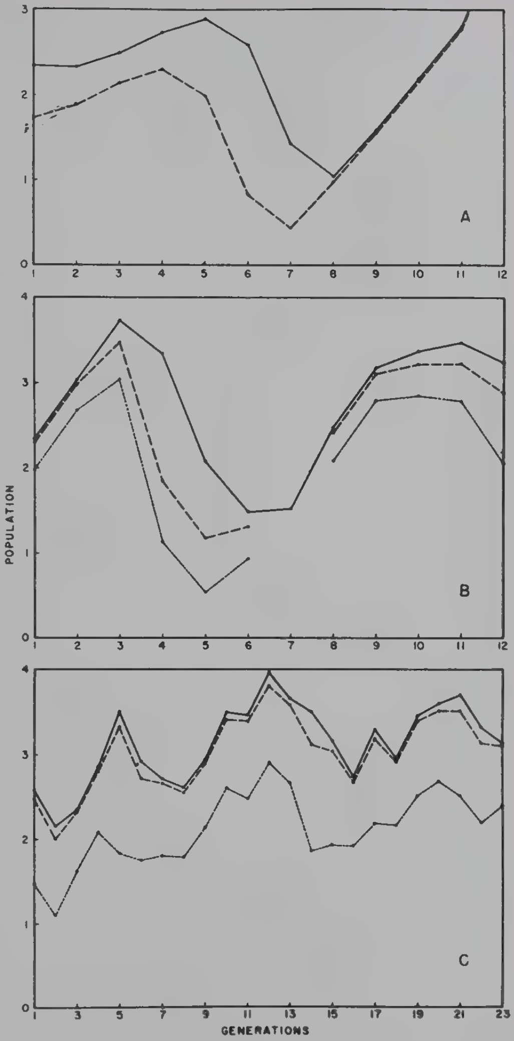


Fig. 1. Population and survival trends for successive generations, expressed as common logarithms. Solid lines represent population, h_n; broken lines represent survival, $s_n = h_n\,(1 - k_n)$, after population is reduced by parasitism, k_n; and dotted lines represent adjusted survival, $s'_n = h_n\,(1 - c)\ (1 - k_n)\ (1 - qk_n)$, based on an assumed interaction between parasitism and other factors (see text). A—Nicholson and Bailey model; B—Black-headed budworm; C—European spruce sawfly.

Black-headed Budworm

The black-headed budworm is a native tortricid that periodically causes noticeable defoliation of fir

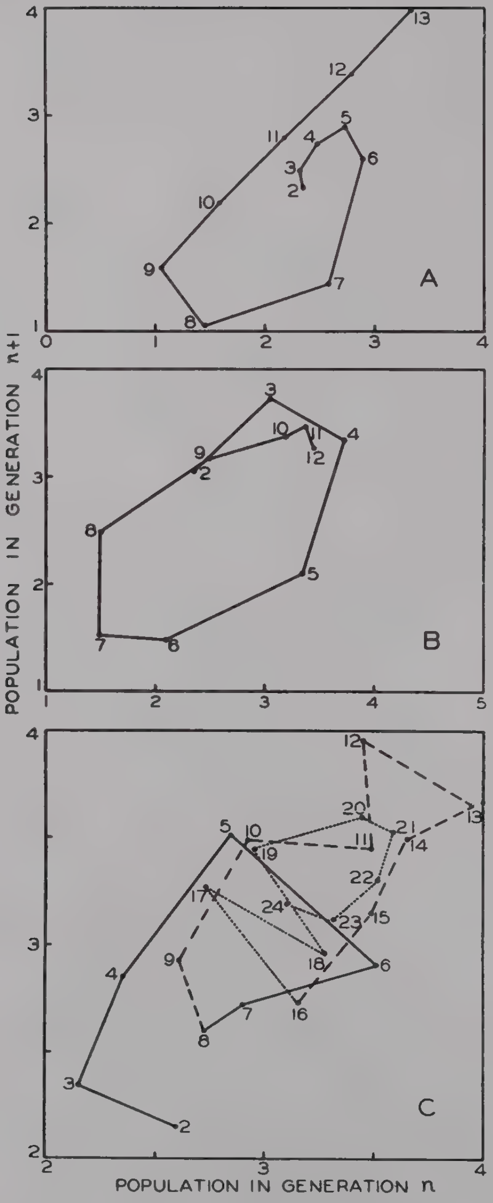


FIG. 2. Population in generation n + 1 in relation to population in generation n, with both expressed as common logarithms. The numerals beside the plotted points refer to the successive n + 1 generations. A—Nicholson and Bailey model; B—Black-headed budworm; C—European spruce sawfly.

and spruce. In New Brunswick, however, high populations decline before any trees are killed and before food shortage becomes an important factor in the decline. There is one generation a year and the winter is passed in the egg stage. Since 1946 larval population has been measured each year in a coniferous stand in northern New Brunswick by the branch-surface method already described in detail for the spruce budworm (Morris 1955). The black-headed budworm is attacked by a rather large complex of Ichneumonidae and Tachinidae but the individual species will not be discussed because only total parasitism, as determined by the dissection or rearing of the larval samples, will be used in the analysis. The population figures for both the budworm and the sawfly (Table I) have been multiplied by ten in order to avoid the inconvenience of negative logarithms in later stages of the analysis.

TABLE I. Larval population density and per cent parasitism in successive generations of the black-headed budworm and European spruce sawfly. Sawfly populations in the summer generations (the odd numbers in the first column) have been multiplied by 2.8 before tabulation for reasons discussed in the text

Generation	BLACK-HEADED BUDWORM		EUROPEAN SPRUCE SAWFLY	
	Population per 100 sq. ft. of foliage	% parasitism	Population per 100 trees	% parasitism
1	22	7	39	21
2	112	9	14	30
3	533	43	22	1
4	225	97	70	6
5	12	88	327	35
6	3.1	31	81	37
7	3.3	?	53	13
8	31	14	41	14
9	150	10	84	6
10	237	28	307	17
11	300	44	285	16
12	183		907	30
13			448	16
14			307	60
15			140	25
16			53	11
17			190	21
18			88	10
19			280	14
20			393	21
21			532	25
22			200	35
23			129	2
24			150	

As the records to date cover only 12 generations, no firm conclusions about population cycles can be reached. However, the population trend during this period (Fig. 1B) does not support the idea of random cycles, since the interval of 8 generations between peaks would rarely be expected in a series of random numbers (Cole 1954). The broken line again represents s_n, or the population of larvae that were not parasitized, and the

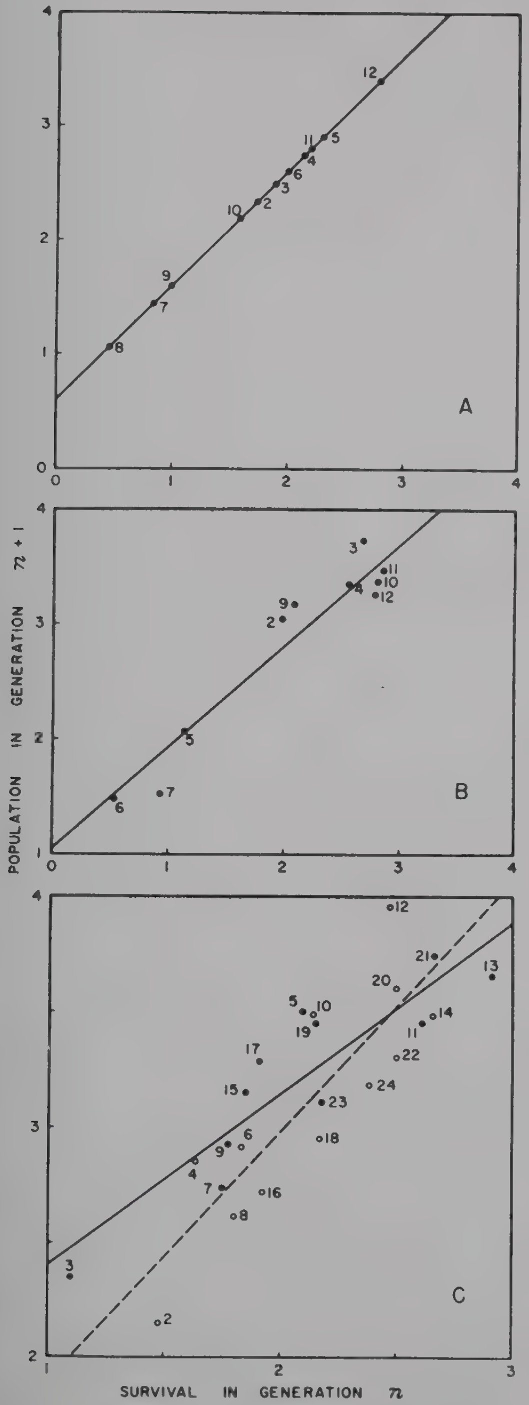


FIG. 3. Population in generation $n + 1$ in relation to survival in generation n, with both expressed as common logarithms. The numerals beside the plotted points refer to the $n + 1$ generations. A—Nicholson and Bailey model; B—Black-headed budworm; C—European spruce sawfly, with even numbers representing fall generations and odd numbers summer generations. Adjusted survivals (s'_n) have been used in both B and C (see text).

dotted line below it will be explained later. Parasite data are lacking for Generation 7.

When log h_{n+1} is plotted over log h_n (Fig. 2B) the figure is a closed one which doubles back upon itself. If the points are treated as a scatter diagram, there is a correlation of $r = .67$ between log h_{n+1} and log h_n. Now let us assume that h is affected by a factor that causes a constant percentage mortality in each generation; in other words, a factor that would play no role in population variation in a given place and would have no predictive value. When h_n is reduced by such a mortality to get s_n, the plotting of log h_{n+1} over log s_n will give a figure of the same size and shape as the plotting of log h_{n+1} over log h_n, but the new figure will be moved a certain distance to the left, depending upon the magnitude of the mortality. Since $\log s_n = \log h_n + \log (1 - k_n)$, log h_n has simply been changed by a constant. Also, the same correlation of $r = .67$ will now exist between log h_{n+1} and log s_n. The reason for considering the relation between log h_{n+1} and log h_n will now be clear. A suspected key factor will be of no value unless it permits better prediction than could be made from h_n alone. That is, the relation between log h_{n+1} and log s_n for the black-headed budworm should be tested against $r = .67$, not against $r = 0$.

When larval parasitism is tested as a possible key factor, the correlation between log h_{n+1} and log s_n is $r = .93$. This is the correlation obtained when the broken line of Figure 1B is moved one generation to the right and compared with the solid line. The degree of improvement over $r = .67$ can be best appreciated by considering r^2, and this suggests that 45% of the variance is accounted for when log h_n is used for prediction as compared to 86% when log s_n is used. The relative effects of log h_n and log s_n on log h_{n+1} could be partialled out by a more sophisticated correlation analysis, but this is not considered advisable for present purposes. For one thing, the points representing log h_{n+1} plotted over log h_n have been treated like the points in a scatter diagram, whereas in fact they have a pattern (Fig. 2B). For another, if parasitism is directly responsible for this pattern, as is highly probable, it would not be biologically meaningful to say that a certain part of the high correlation can be attributed to h_n and another part to s_n.

The regression line has not been plotted in Figure 3 because further improvements in the degree of correlation through an adjustment in s_n will be considered in a later section. However, the regression formula is $\log h_{n+1} = .53 + .92 \log s_n$. The effective rate of increase of the black-headed budworm when parasitism is very low appears to be roughly $F = 5$ (Table 1). Therefore, if parasitism were a perfect key factor we should expect $\log h_{n+1} = .70 + \log s_n$. The estimated slope of $b = .92$ is significantly different from $b = 0$ but not significantly different from the expected slope of $b = 1$. Nor is the estimated intercept of .53 significantly different from the expected $\log F = .70$, although it should be noted that the number of points is too small to provide reliable estimates of either F or b. In any case, close agreement with the model in these respects is scarcely to be expected, since there are probably no perfect key factors in nature, and it will be more profitable to attempt to interpret the differences that are observed. For example, if the slope of $b = .92$ proves with additional data to be significantly less than unity, it suggests that other mortality factors besides the selected key factor are operating more severely against the population at high densities. That is, as s_n increases, the observed value of h_{n+1} becomes progressively lower than would be expected from the effects of a perfect key factor with a slope of unity.

To summarize for the black-headed budworm it seems clear that parasitim is, indeed, a key factor and can be used to predict host population with a reasonable degree of accuracy. The prediction equation has a standard deviation from regression (= standard error of estimate) of .31. The high degree of correlation is rather surprising, especially in view of the fact that larval parasitism, as will be shown later, contributes a rather small proportion of the total mortality that occurs in each generation of the insect. It would seem that the black-headed budworm was remarkably insensitive to random variations that must have occurred in other factors during the limited number of generations that have been studied to date. The next example will illustrate such random influences to a much greater degree.

EUROPEAN SPRUCE SAWFLY

The European spruce sawfly is an introduced insect and its population in New Brunswick forests was clearly limited only by the supply of spruce foliage until natural enemies were introduced from Europe. The collapse of high populations was largely the result of a virus that appears to have been introduced in shipments of parasites. After the collapse, however, two of the introduced parasites—*Drino bohemica* Mesn. (Tachinidae) and *Exenterus vellicatus* Cush. (Ichneumonidae)—became more effective, at low population levels, than disease. The combined parasitism caused by these two species will be used as the suspected key factor in the present analysis. Twenty years' data are now available for permanent plots in central New Brunswick but I propose to use only the records subsequent to 1946, after the influence of virus declined and populations began to oscillate at a low level. Larval populations are assessed each generation by "beating" small trees with a pole at intervals of a week or so. The larvae thus dislodged are collected from a canvas sheet on the ground, counted, and taken to the laboratory for diagnosis of parasitism and disease. For present purposes only the three samples taken at or near the peak larval population of each generation will be used (Table I).

The summer generation of the sawfly comes from overwintering cocoons and most of the cocoons and parasites produced by the summer generation give rise to a second, or fall, generation. A smaller proportion of the cocoons and parasites of the first generation may remain in diapause until the following year, but for simplicity in the present analysis it will be considered that the sawfly has two generations a year. When disease is not prevalent there is a fairly constant numerical relationship between these two generations and in the larval stage the population in the fall generation averages 2.8 times as high as that in the summer generation. The population figures for the summer generations have all been multiplied by this factor in order to avoid the complications that would otherwise arise.

The population trend (Fig. 1C) is not as smooth as the corresponding trend for the black-headed budworm. However, although there is a considerable difference of opinion as to the interpretation of cycles, it seems reasonable to suppose that three cycles are represented with peaks in Generations 5, 12 and 21 and lows in Generations 2, 8 and 16. On this basis the cycle length is about the same as that of the black-headed budworm, although the oscillations are less violent.

When $\log h_{n+1}$ is plotted over $\log h_n$ polygons are again formed (Fig. 2C, with different types of lines corresponding to the three cycles). However, they are rather irregular, particularly because of the increase in population between Generations 11 and 12 and the decrease between Generations 17 and 18. Further, the polygons do not follow the same course but suggest a gradual rise in mean population. This is apparent from a comparison of the inflection points where a falling population starts to rise again (Generations 2, 8, 16 and 23). If this increase in mean population continues the sawfly may again reach a density at which virus disease becomes more effective than parasites.

In considering the relation between log h_{n+1} and log s_n it is necessary to separate the summer and fall generations because the data indicate that two different regression lines are involved. The cocoons and parasites of the fall generation overwinter in the ground, where they are exposed for a longer period than the cocoons and parasites of the summer generation. Also, diapause in the summer generation affects the population density of the fall generation. It is understandable, therefore, that the regressions between h_{n+1} and s_n are different for the two situations, despite the fact that population density in the summer generations has been adjusted to make it comparable to population density in the fall generations. The relation between log h_{n+1}, log h_n, and log s_n (Table II) is therefore shown separately for the two situations: first, where n + 1 represents fall generations and n represents summer generations and, second, where n + 1 represents summer generations and n represents fall generations.

TABLE II. The correlation and regression statistics for the black-headed budworm and European spruce sawfly when population density in the next generation (log h_{n+1}) is predicted from: (1) population density in the present generation (log h_n); (2) survival from larval parasites in the present generation (log s_n); (3) adjusted survival (see text) in the present generation (log s'_n)

Statistic	Relation between log h_{n+1} and log:	Black-headed budworm	EUROPEAN SPRUCE SAWFLY n+1= fall generation	EUROPEAN SPRUCE SAWFLY n+1= summer generation
Correlation coefficient (r)	h_n	.67	.62	.73
	s_n	.93	.68	.83
	s'_n	.96	.85	.90
Intercept (log F)	h_n	.63	.87	1.40
	s_n	.53	.55	1.17
	s'_n	1.03	.79	1.66
Slope (b)	h_n	.78	.70	.59
	s_n	.92	.83	.69
	s'_n	.87	1.09	.74
S.E. of estimate	h_n	.65	.41	.30
	s_n	.31	.38	.25
	s'_n	.25	.28	.20
Value of q which gives maximum r	s'_n	.6	2.4	1.2

Comparison of the correlation coefficients in Table II indicates that the predictive value of parasitism is little better than the predictive value of h_n, a conclusion that would be supported by an ocular comparison of the solid and broken trends in Figure 1C. Survival from parasites appears to be somewhat higher during periods when sawfly population is increasing but, in general, appears merely to follow the trend of host population. The fall generation is the less predictable one, possibly because of the effects of a variable degree of diapause. Also, the intercepts for the regression lines are too high (Table I suggests F = 3-4) and the slopes too low, suggesting that other mortality factors besides parasites are responding to changes in sawfly population.

SURVIVAL ADJUSTMENT

As a suspected key factor, then, parasitism has a relatively high predictive value in the case of the black-headed budworm but a much lower predictive value in the case of the European spruce sawfly. One possible explanation for the difference is that percentage parasitism reaches considerably higher values for the budworm than it does for the sawfly (Table I). It has been demonstrated elsewhere, however, that a factor causing a low degree of mortality can have as great an effect on population trend as one causing a high degree of mortality, providing it is operating during a period in the life cycle when other factors ("contemporaneous factors") are causing high mortality (Morris 1957). Therefore, before accepting this explanation, it may be of interest to see whether the survival estimates can be adjusted in some way to make allowance for the effects of other mortality factors.

In the example of the model, parasitism was assumed to be the only variable factor operating, so the survival formula $s_n = h_n (1 - k_n)$ was appropriate. In the natural examples, however, it is known that other factors were operating at the same time as the parasites, some of them causing a variable and some a relatively constant degree of mortality. Thus the effect of parasitism on survival is not adequately represented by the formula. The larval stage is a very dynamic stage in the life of most defoliators and during the period when parasites are inside the host mortality from other factors is usually rather high. Even when parasitism is very low, field data suggest that mortality during this period is rarely less than 50% in populations of the budworm and 80% in populations of the sawfly. This mortality will be represented by 'c' and it will be assumed that it is relatively constant from generation to generation, particularly in the sense of being density independent. The effect of c is contained in F because c helps to determine the effective rate of increase from generation to generation when $k = 0$. However c also influences the effect of k on survival, both by increasing the general level of contemporaneous mortality at which k operates and by "competing" with k in the killing of insects. There is another type of mortality which, like k, is related to population density. Budworm larvae, whether parasitized or not, are eaten by birds, while sawfly populations are reduced by disease and birds in the trees and by small mammals on the ground. This mortality will be represented by 'qk' on the assumption that it varies in the same way as k. Its effect is not contained in F because $qk = 0$ when $k = 0$.

If these mortalities were additive, the survival formula could be re-written: $s'_n = h_n [1 - (c + k_n + qk_n)]$. It is clear that they are not additive, however, for when the variate values of k (Table I) are added to the mean values of c given above, mortality in some years considerably exceeds 100% for both insects. Allowance must be made for the fact that mortality factors interfere with one another in their effect on natural populations. Some of the budworm and sawfly larvae containing parasites are eaten by predators, for example, or killed by adverse physical factors. According to the multiplication theorem of the calculus of probabilities, the probability of none of two or more events occurring is equal to the product of their individual probabilities of non-occurrence. Thus, if parasitized and nonparasitized larvae are equally vulnerable to mortality from other factors, survival can be better adjusted as follows:

$$s'_n = h_n (1 - c) (1 - k_n) (1 - qk_n)$$

This represents a very great over-simplification of interactions that are often very complex. Further, in the absence of detailed life-table data, other modes of interaction might equally well be postulated. The present analysis, however, is more concerned with prediction than with the elucidation of ecological principles and if s'_n has consistently better predictive value than s_n, its use is obviously justified.

In calculating $\log s'_n$ from the above formula it is not necessary to have a value for c because it is treated as a constant and does not affect the degree of correlation between $\log h_{n+1}$ and $\log s'_n$. However, in view of the fact that it provides more realistic survival values, c has been retained in the following analysis, with values of .5 for the budworm and .8 for the sawfly. The value of q has been estimated by trial and error as the value which maximizes correlation between h_{n+1} and s'_n. As q is increased, r increases systematically to a certain maximum value and then decreases rather abruptly. The fact that larger values of q are obtained for the sawfly (Table II) seems reasonable, because it is known that other density-related factors such as disease and predation are much more important in sawfly populations than in black-headed budworm populations.

The adjustment to survival has increased the degree of correlation and reduced the error of estimate in all cases, particularly for the sawfly (Table II). It has also brought the slope of the regression lines closer to unity, as would be expected, by compensating for the effect of other density-related factors. However, although the estimated values of F have been listed, they are no longer applicable in the sense in which F was originally defined because c, already contained in F, was repeated in s'_n.

The new survival trends (dotted lines in Fig. 1), in comparison to the old, provide a visual impression of the manner in which the adjustment has improved correlation. The differential between population and survival has been increased during the periods of declining population, when total mortality is high and the contemporaneous factors are exerting their greatest influence.

Although it is necessary to separate the summer and fall generations of the sawfly for purposes of estimating q, the regression diagrams (Fig. 3) suggest that they might now be combined without seriously decreasing the predictive value of s'_n. The deviations from regression (Fig. 3B, 3C) result partly from the fact that F and c, which no doubt vary considerably because of climate, are assumed to be constant, and partly from sampling errors in measuring both h and k.

Finally, the scatter about these regression lines suggests that the logarithmic transformation has been successful in stabilizing variance. If the ordinate is mentally anti-logged, it will be clear that a valid regression analysis would not have been possible in terms of the original variates. At the same time it is well to remember that the standard errors of estimate in Table II apply only to the logarithmic scale; on the scale of the original variates they represent errors of estimate that increase rapidly in absolute value (though not in percentage value) as population density increases.

Discussion

The analysis has been concerned only with those changes in population that occur from generation to generation and it is therefore of interest to see what portion of total generation mortality may be attributed to the key factors. A mated female of the black-headed budworm may lay 60 eggs, from which about 20 larvae may survive to the sampling period. A generation mortality of 58/60 or about 97% is necessary to prevent an increase in population. When larval parasitism reaches the level of about 40% (*i.e.*, 8 of the 20 larvae) a rising population trend is reversed. In terms of the whole generation, therefore, parasitism need provide only 8/60 or about 13% mortality in order to prevent an increase in population.

The sawfly lays 45 eggs and survival to the sampling period is 22 larvae. Since this species is thelytokous the required generation mortality is 44/45 or 98%, and population generally starts to fall when larval parasitism reaches the vicinity of 16% (*i.e.*, 3.5 of the 22 larvae). So parasitism need provide only 3.5/45 or 8% mortality in terms of the whole generation. These are only approximations but even if they prove to be somewhat too low, it is remarkable that a factor contributing so little to total mortality is of value in predicting population changes from generation to generation. No doubt one explanation, especially in the case of the sawfly, is the possibility that the suspected key factor provides an index to the action of a number of factors that have the same sort of response to changes in population density. The importance of disease and predation in sawfly populations has already been mentioned. Although caution must be used in placing any rigid interpretation on q, its estimated values for the sawfly (Table II) suggest that these other factors contributed more mortality than did the two parasites selected for the analysis. Similarly, if only one or two of the parasites attacking the black-headed budworm had been used instead of the whole complex, their predictive value might have been equally good and the effect of the other parasites might have been revealed as an increase in the value of q.

A key factor was defined as any mortality factor that has useful predictive value and no attempt has been made to establish cause and effect, because single-factor data are scarcely suitable for this purpose. More intensive work on the black-headed budworm has not yet revealed other factors that are operating in a way to produce the observed population changes, however, and it seems likely that we are dealing with host-parasite oscillations. There is ample evidence that the European spruce sawfly was limited only by its food supply in Eastern Canada until parasites and disease were introduced so, again, there seems little doubt that these factors, probably aided by predation, were the regulating influence during the period covered in the present analysis. For both species, however, the data should be extended over additional cycles before final conclusions are drawn. Even in simple, controlled laboratory experiments in which only one suspected key factor is allowed to vary, firm conclusions would scarcely be possible after the study of so few generations.

After records have been accumulated for additional generations, it should be possible to refine the survival adjustment and to test the effects of alternative assumptions on interference. The use of $(1-c)(1-k)(1-qk)$ in the present analysis is arbitrary and no real biological significance should be attached to it. The use of $(1-c-k)$ or $(1-qk)$, with maximum mortality arbitrarily set at 99%, or the hyperbola $1-k/(k+.01)$, give improvements in correlation that are almost equally good. Although they have less appeal, biologically, than the formula that was used, there are insufficient degrees of freedom for statistical tests. About all that can be said is that prediction is improved by making some adjustment for the effect of associated mortality, so long as this adjustment makes provision for mutual interference among difference factors, particularly when total mortality becomes high. The interaction between different mortality factors, which could be an important factor in the conservation of species, has received little attention to date. Its importance may be appreciated by considering the number of generations (Table I) in which the effects of c, k, and qk, would exceed 100% if they were additive. Very detailed, multi-factor studies are required for the elucidation of interactions and should be preferred to single-factor studies whenever they are feasible.

It will be interesting to learn whether or not single-factor data have useful predictive value for other species. Although many entomologists have been impressed by the multiplicity of factors contributing to population change, the fact that most insect population work has been done during outbreak periods, when economic values are threatened, has biased our thinking considerably. It is true that a confusing array of over-population phenomena are involved in the crash of outbreak populations, but large-scale outbreaks represent the exception in population behavior rather than the rule. Although a very few native defoliators, like the spruce budworm, periodically "escape" their regulating influences, by far the great majority of foliage insects never reach the limit of their food supply. The data used to illustrate the present analysis may therefore be considered more representative of normal population behavior than data collected during an outbreak.

In the examples presented here each defoliator was studied in only one forest stand, while population surveys indicated that the oscillations in population were taking place at considerably higher, or lower, mean densities in other types of stands not far away. The extension of single-factor analysis to a variety of stand types might suggest useful leads to more intensive work on the role of stand factors and physical environment in the determination of mean density. Differences in the slope of the regression lines and in the value of F from stand to stand would be of considerable interest. However, a detailed multi-factor study would be necessary both to segregate the effects of different environmental factors and to permit conclusive tests of different population theories. Thus the single-factor approach should be recognized as a useful lead to more complete studies but certainly not as a substitute for them.

SUMMARY

Examples of single-factor analysis are presented for natural populations of two defoliating insects that are common in the coniferous forests of New Brunswick. One is the native black-headed budworm, *Acleris variana* (Fern.), and the other the introduced European spruce sawfly, *Diprion hercyniae* (Htg.). Population density was measured at one point in the larval stage in each generation and the analysis is concerned only with population changes from generation to generation. The larvae collected during population sampling were dissected or reared to determine the percentage parasitism, and the object of the analysis was to learn whether parasitism, as a suspected 'key factor,' could be used effectively to predict population density in the next generation. Parasitism was found to have high predictive value for the budworm but a lower predictive value for the sawfly. Prediction was improved, however, when adjustments were made to make allowance for the effects of associated mortality factors and for the interference between these factors and parasitism. In the case of the sawfly, at least, there is reason to believe that parasitism derives part of its predictive value from the fact that it indicates the mode of action of associated factors having a similar type of response to changes in population density. It is concluded that parasitism is a key factor in the two populations, in the sense that it has useful predictive value, and that single-factor analysis can provide valuable leads to more intensive and conclusive multi-factor investigations.

Acknowledgments

I am very much indebted to C. A. Miller and D. E. Elgee of the Forest Biology Laboratory, Fredericton, for permitting the use of certain unpublished data; to D. G. Mott and K. E. F. Watt for valuable criticism; and particularly to the Editors of Ecology for detecting a mathematical artifact in the first draft of the paper and making helpful suggestions for improvement.

REFERENCES

Cole, L. C. 1954. Some features of random population cycles. J. Wildl. Mgt. **18**: 2-24.

Morris, R. F. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. Can. J. Zool. **33**: 225-294.

———. 1957. The interpretation of mortality data in studies on population dynamics. Can. Ent. **89**: 49-69.

Nicholson, A. J. and V. A. Bailey. 1935. The balance of animal populations. Proc. Zool. Soc. London. 1935, pp. 551-598.

STUDIES ON THE PHYSIOLOGICAL VARIATION BETWEEN TROPICAL AND TEMPERATE ZONE FIDDLER CRABS OF THE GENUS *UCA*

I. THERMAL DEATH LIMITS[1]

F. John Vernberg[2] and Richard E. Tashian[3]
Duke University Marine Laboratory, Beaufort, N. C. and Duke University, Durham, N. C.

Fiddler crabs (Genus *Uca*) are distributed over most of the eastern coastline of the Americas and the islands of the Caribbean (Rathbun 1918). Although all species have either tropical or temperate zone affinities, there is an area of overlap of some northern and southern forms along the east coast of Florida. In investigating various physiological responses of these fiddler crabs, it is hoped that a clearer picture of the role of physiology in the distribution and ecology of these organisms will be obtained. The present paper in this series is undertaken both to determine the upper and lower thermal death limits of various species of tropical and temperate zone fiddler crabs and to study the influence of acclimation to low temperature on shifting the thermal death points. By using thermal acclimation studies it is possible to determine better whether any difference in response can be explained on the basis of genotypic or phenotypic variation.

Methods and Materials

When this study was begun, *Uca pugnax* consisted of a northern race, *U. pugnax pugnax*, and a southern race, *U. pugnax rapax*. However, on the basis of morphological and physiological differences, these two races have been separated into two distinct species (Tashian and Vernberg 1958) with the northern race now being *U. pugnax* and the southern one *U. rapax*. Although detailed studies of the thermal death points were made on these two species, some determinations were also made using other tropical and temperate zone species. The tropical species used were *U. rapax*, *U. thayeri*, *U. mordax*, and *U. leptodactyla*, and those from the temperate zone were *U. pugnax*, *U. minax*, and *U. pugilator*.

Animals used in this study were collected from 3 geographical areas: Beaufort, North Carolina, Miami, Florida, and Jamaica, B.W.I. In Jamaica, *rapax* and *mordax* came from Port Henderson, while *leptodactyla* were from the swamp near Morant Point Lighthouse, and *thayeri* from Port Morant. Studies involving animals from Beaufort, North Carolina and Miami, Florida were conducted during the period from May to August, 1957, while the Jamaican forms were investigated from October to December, 1957. Crabs were collected and brought back to the laboratory where they were maintained in aquaria containing about one inch of sea water. The animals were exposed to food (Pablum and pieces of fish) and appeared to be in a good nutritional state at the time of experimentation.

Three to five animals were placed in a 250 cc Erlenmeyer Flask containing about 10 cc of sea water. The flask had been submerged in a temperature controlled water bath for about 15 minutes before animals were introduced to allow for thermal equilibration. Animals were exposed to the experimental temperature for given periods of time after which they were removed from the flask and the number of surviving animals was determined. An animal was considered as being a non-survivor if it could not right itself after being placed on its back. Each animal was observed up to 24 hours after exposure to a particular temperature before being called a non-survivor.

In the case of *pugnax* and *rapax*, 2 sets of animals were used. One group had been kept at 15° C for 7-10 days ("cold-acclimated animals"), and a second group consisted of animals collected from the field and maintained in the laboratory at temperatures which varied from about 23-27° C ("room-animals"). On the basis of the work of Spoor (1955) on crayfish and Brett (1946) on goldfish, this period of 7-10 days' acclimation to cold was deemed sufficiently long to have exerted any major significant influence on thermal death points. It should be noted that the temperature in the field at the time of collecting was very similar for all 3 study areas although the work in Jamaica was done later in the year. Thus, all the room-animals from the 3 areas appeared to have similar recent thermal histories.

Two high temperatures were used (42° and

---

[1] Supported by a grant (G-2509) from the National Science Foundation. Grateful acknowledgment is made to the University College for the West Indies, Jamaica, B.W.I. and to the Marine Laboratory, University of Miami for supplying laboratory space for portions of this work.

[2] A portion of this work was done while serving as a John Simon Guggenheim Memorial Fellow.

[3] Present address: Department of Human Genetics, University of Michigan.

44° C) in order to observe a representative segment of the temperature-time response curve of both the tropical and temperate zone species. To determine the cold death points, observations were made at 7° C on both tropical and temperate zone forms and lower temperatures were used only for animals for North Carolina.

RESULTS

Table I represents the results of heat death point determinations of *pugnax* from Beaufort, North Carolina and *rapax* from both Miami, Florida and Port Henderson, Jamaica. A more graphic but less detailed representation of these data is shown in Figures 1 and 2. It appears that *rapax* is more tolerant of high temperature than the more northern species, *pugnax*. Florida crabs responded more like Jamaica forms than like *pugnax* from North Carolina. When exposed to 42° C the southernmost species withstood longer periods of exposure than did the northern form. The response of the Miami crabs at this temperature is unlike either of the other groups, *i.e.*, there is no significant increase in mortality above the 50% level until after exposures of 80-90 minutes. Comparable increases occurred between 40-50 minutes for Jamaican animals, and between 35-40 minutes for North Carolina fiddler crabs.

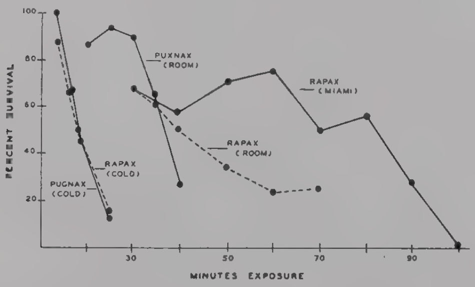


FIG. 1. Time to death at 42° C of *Uca pugnax* and *U. rapax* acclimated to 15° C and room animals.

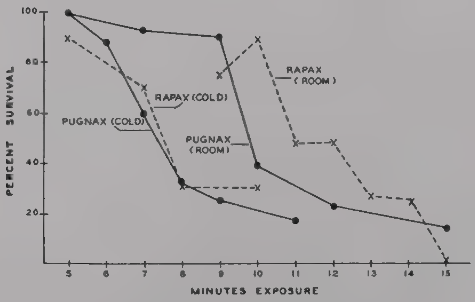


FIG. 2. Time to death at 44° C of *Uca pugnax* and *U. rapax* acclimated to 15° C and room animals.

TABLE I. Heat death point determinations of Fiddler Crabs from tropical and temperate zones

time in minutes	42° C number of animals	% surviving	time in minutes	44° C number of animals	% surviving
Uca pugnax from Beaufort, N. C.					
Room Animals					
20	13	85	5	6	100
25	15	93	7	15	93
30	29	89	9	10	90
35	46	63	10	49	39
40	46	26	12	31	23
			15	7	14
Cold Acclimated Animals					
	42° C			44 °C	
12	26	100	5	8	100
15	18	67	6	8	88
18	18	44	7	15	60
25	9	11	8	13	31
			9	20	25
			11	12	17
Uca rapax from Miami, Florida					
Room Animals					
	42° C			44° C	
30	12	67	8	12	67
40	16	56	10	12	67
50	16	69	12	12	17
60	12	75	14	12	25
70	12	50	15	12	17
80	9	56	16	12	8
90	8	25	17	12	0
100	8	0	18	12	0
Uca rapax from Jamaica, B. W. I.					
Room Animals					
	42° C			44° C	
30	6	67	9	8	75
35	15	60	10	9	89
40	43	49	11	50	48
50	16	31	12	25	48
60	18	22	13	19	26
70	13	23	14	4	25
			15	5	0
Cold Acclimated Animals					
	42° C			44° C	
12	8	88	5	10	90
15	12	66	7	10	70
18	20	50	8	10	30
25	15	13	10	10	30

It was quite apparent that acclimation to 15° C before exposure to high temperature had a profound influence on the response of these species. Both *pugnax* from North Carolina and *rapax* from Jamaica showed similar responses. The 50% mortality level was reached after about 18 minutes exposure to 42° C, while similar figures for room animals from Beaufort was 35-40 minutes and from Jamaica 40-50 minutes. At 44° C cold-acclimated animals also responded in a distinctly different manner from room-animals. Cold-acclimated animals were more temperature sensitive. Interspecific differences noted when room-animals were studied disappeared in experiments using cold-acclimated individuals. It would appear that within the limits of these experiments tropical crabs exhibit a greater range of response than temperate zone forms. As noted above tropical crabs could withstand high temperature longer than northern forms, but when cold-acclimated animals were used both groups responded similarly.

At low temperatures a very dramatic species difference was noted. Animals from North Carolina could withstand continuous exposure to 7° C for at least 2 weeks with a low mortality rate, while Jamaican animals died after short exposures to this temperature (Table II). Table III shows the response of room animals from North Carolina to exposures of 3.5° C for various periods of time. At the end of 4½ days at 10° C, 20 specimens of *rapax* from Miami, Florida were dead, while a similar group of *pugnax* from North Carolina were alive after 3 weeks.

Table II. Response of *Uca rapax* from Jamaica, B.W.I. to exposure to 7 C for different periods of time

Duration of exposure (minutes)	Number of animals	% Surviving
Room Animals		
10	10	80
20	10	70
30	10	60
40	10	40
53	7	29
60	7	0
70	7	0
Acclimated to 15 C (7 days)		
20	10	100
50	10	60
65	10	20

Table III. Response of *Uca pugnax* from Beaufort, N. C. to exposure to 3.5 C for different periods of time

Duration of exposure (hours)	Number of animals	% Surviving
Room Animals		
2	8	88
3.5	8	75
6	10	70
8-9	44	23
10-11.5	63	24
13	14	14

Although, cold-acclimated *rapax* from Jamaica survived slightly longer exposures to 7° C than non-acclimated animals, a significant shift in response did not occur (Table II). In sharp contrast, *pugnax* from North Carolina showed a markedly different response to low temperature after cold acclimation. Animals first subjected to 15° C for one week could withstand subsequent exposure to 2.5° C for 30 days while room animals reached the 50% mortality level after 6-8 hours at 3.5° C.

Less detailed studies involving other species of fiddler crabs give evidence that the fiddler crabs in one geographical area have similar thermal death limits. Thus, the above described species difference can be correlated with the distributional pattern of these animals; in general, tropical fiddler crabs are less able to tolerate low temperature than temperate zone animals. Other tropical species of *Uca* studied were *mordax, thayeri,* and *leptodactyla.* Of the 10 specimens of each species exposed to 7° C for 35 minutes, only one large individual of *thayeri* survived. However, 5 of the *thayeri* exhibited a reflex response while none of the *leptodactyla* or *mordax* did. Observations on *minax* and *pugilator* from North Carolina indicate that their response to low temperature is similar to that of *pugnax*. Throughout this study no consistent difference in response was observed which could be correlated with size.

Discussion

Temperature is an ecological factor which is extremely significant in determining the distributional limits of some organisms (Andrewartha and Birch 1954). Perhaps because of the technological ease of determining and maintaining temperature, much work has been done on the significance of this factor to the functioning of animals at the various levels of protoplasmic organization. Two recent papers have reviewed much of the literature in this field (Prosser 1955, and Bullock 1955).

In the past few years a number of papers have been concerned with the response of various species of *Uca* to temperature. Although thermal death points were not specifically studied, Scholander *et al.* (1953) noted that *mordax* from Panama could not withstand low temperatures. Tashian (1956), working with populations of *pugnax* and *rapax* which were collected from New York to Trinidad, B.W.I., found marked differences in survival between the tropical and temperate zone species exposed to reduced temperature. Demeusy (1957) observed that *pugilator* from Englewood, Florida could not withstand low temperature as well as *pugilator* from Woods Hole, Massachusetts. It is of interest to note that of the 43 *pugilator* from Florida that this worker subjected to 1.4° C for 5 hours only 18 were dead the next day, whereas when truly tropical species of *Uca* from Jamaica were exposed to 7° C the majority were dead within 40 minutes, and of the 22 *rapax* tested by Tashian (1956) from Florida and Trinidad, none survived a temperature of 5° C for more than 15 minutes. It seems, therefore, that even when a primarily temperature zone species like *pugilator* extends into sub-tropical regions it retains some of its resistance to low temperatures.

The results of Orr (1955) and Teal (1958) on the temperature-time heat death point of temperate zone *Uca* agree well with those of the present paper. No report of similar studies on tropical fiddler crabs has been found in the literature. When comparing the response of these 2 groups of organisms, tropical species survived high temperatures somewhat better than temperate zone forms.

Variations in the physiological response of geographically separated populations of animals have been described and discussed by a number of workers (Sparck 1936, Fox 1936, Thorson 1936, Moore 1949, Johnson 1952, Volpe 1953). The question arises of whether these described variations between populations are due to genotypic or phenotypic differences. Various investigators have emphasized the need for determining the role of acclimation on shifting the limits of response of any particular rate function studied (Fry *et al.* 1942, Hart 1952). In the present study it was shown that, within the limits of the experimental procedure, animals from the tropics could not be acclimated to withstand the same degree of reduced temperature as temperate zone species. Thus, it seems that these observed differences between tropical and temperate zone crabs are genotypic. At elevated temperatures the more southern forms can withstand prolonged higher temperatures better, although it should be noted that after cold acclimation tropical and temperate zone crabs responded alike.

Results of this study strongly suggest that the inability of tropical fiddler crabs to withstand low temperatures would limit their northward spread. Not only do the temperate zone animals survive reduced thermal levels longer than tropical forms but they also have the ability to acclimate to reduced temperatures. This ability to acclimate has real survival value to temperate zone animals. Warm-adapted animals lived a much shorter time at low temperatures than cold-adapted organisms. Thus, at the approach of winter when the temperatures are gradually reduced, the temperate zone *Uca* acclimate and can survive at lower temperatures. This process is reversed with the approach of spring and correspondingly higher ambient temperatures. Although the implications of the response to low temperatures are obvious, the factors curtailing the southward distribution of northern forms need to be studied. One might speculate on the basis of this study that the slightly better ability of southern forms to survive at elevated temperatures might have some adaptive significance.

SUMMARY

In an attempt to understand the role of extremes in temperature in the distribution and ecology of organisms, the upper and lower thermal death limits of several species of tropical and temperate zone fiddler crabs were determined. In addition the influence of acclimation to low temperature in relation to the thermal death limits was studied.

At 42° and 44° C tropical species survived somewhat longer than temperate zone forms. After acclimation to 15° C for 7-10 days, interspecific differences disappeared and the 50% mortality level was reached sooner.

Marked differences in survival at low temperatures were observed. Tropical species were less cold resistant, and 50% mortality occurred after 30-40 minutes exposure to 7° C; temperate zone animals survived at least 2 weeks at this temperature. Northern species exhibited great lability in acclimating to low temperature while tropical animals were little influenced by acclimation to cold.

These findings suggest that the distribution of fiddler crabs is influenced by their ability to withstand extreme temperatures.

REFERENCES

Andrewartha, H. G. and L. C. Birch. 1954. The distribution and abundance of animals. Chicago, Univ. Chicago Press.

Brett, J. R. 1946. Rate of gain of heat-tolerance in goldfish (*Carassius auratus*). Publ. Ont. Fish. Res. Lab. No. 64: 5-28.

Bullock, T. H. 1955. Compensation for temperature in the metabolism and activity of poikilotherms. Biol. Rev. 30: 311-342.

Demeusy, N. 1957. Respiratory metabolism of the fiddler crab *Uca pugilator* from two different latitudinal populations. Biol. Bull. 113: 245-253.

Fox, H. M. 1936. The activity and metabolism of poikilothermal animals in different latitudes. I. Proc. Zool. Soc. London 1936: 945-955.

Fry, F. D. J., J. R. Brett and G. H. Clawson. 1942. Lethal limits of temperature for young goldfish. Rev. Canad. de Biol. 1: 50-56.

Hart, J. S. 1952. Geographic variations of some physiological and morphological characters in certain fresh-water fish. Publ. Ont. Fish Res. Lab. 72: 1-79.

Johnson, D. S. 1952. A thermal race of *Daphnia atkinsoni* Baird, and its distributional significance. J. Anim. Ecol. 21: 118-119.

Moore, J. A. 1949. Geographic variation of adaptive characters in *Rana pipiens* S. Evolution 3: 1-21.

Orr, P. R. 1955. Heat death. I. Time-temperature relationships in marine animals. Physiol. Zool. **28:** 290-294.

Prosser, C. Ladd. 1955. Physiological variation in animals. Biol. Rev. **30:** 229-262.

Rathbun, M. J. 1918. The grapsoid crabs of America. Bull. U.S. Nat. Museum 97.

Scholander, P. F., W. Flagg, V. Walters, and L. Irving. 1953. Climatic adaptation in arctic and tropical poikilotherms. Physiol. Zool. **26:** 67-92.

Sparck, R. 1936. On the relation between metabolism and temperature in some marine lamellibranches, and its zoogeographical significance. Biol. Medd. **13:** No. 5.

Spoor, W. A. 1955. Loss and gain of heat-tolerance by the crayfish. Biol. Bull. **108:** 77-87.

Tashian, R. E. 1956. Geographic variation in the respiratory metabolism and temperature coefficient in tropical and temperate forms of the fiddler crab, *Uca pugnax*. Zoologica **41:** 39-47.

——— **and F. J. Vernberg.** 1958. The specific distinctness of the fiddler crabs *Uca pugnax* (Smith) and *Uca rapax* (Smith) at their zone of overlap in northeastern Florida. Zoologica **43:** 89-93.

Teal, J. M. 1958. Distribution of fiddler crabs in Georgia salt marshes. Ecology **39:** 185-193.

Thorson, G. 1936. The larval development, growth, and metabolism of arctic marine bottom invertebrates compared with those of other seas. Medd. Grnland **100:** No. 6.

Volpe, E. P. 1953. Embryonic temperature adaptations and relationships in toads. Physiol. Zool. **26:** 344-354.

THE UPLAND FORESTS OF OKLAHOMA[1]

Elroy L. Rice and Wm. T. Penfound
Department of Plant Sciences, University of Oklahoma, Norman, Okla.

Introduction

Objectives

A series of investigations on the deciduous forest frontier was inaugurated in 1953 at the University of Oklahoma. Initially it was planned to confine the studies to the blackjack-post oak forest, the major forest type of the forest-prairie ecotone. Subsequently it became necessary to include all of the upland forest types throughout the state. This report includes analytical data, obtained in the summer months from 1953 through 1957, from 208 upland forest stands. Objectives comprised the identification and distribution of all relatively undisturbed forest types and a quantitative description of each stand based on the woody species. No data were obtained on herbaceous plants because of the necessary variation in time of sampling and the unequal amount of grazing in the diverse stands. During the last two years of the investigation, data were secured on the death of trees caused by the extended drought (1952-1956).

Nature of Oklahoma forests

The upland forests of Oklahoma constitute a westward extension of the oak-hickory association of the deciduous forest formation. According to Braun (1947) the oak-hickory forest developed ". . . from the mixed forest of the tertiary or from the quaternary representative . . . as a result of increasing aridity in Pliocene time, which eliminated the more mesophytic genera . . . from much of the area west of the Appalachian plateau." In 1950, Braun indicated that "To the south and west of the Interior Highlands is an area occupied by oak-hickory forest, oak and oak-hickory savannah, and in part by prairie." Braun thus recognized an east-west cline of oak-hickory forest, oak-hickory savannah, and oak savannah. These savannahs apparently were much more open than they are today. Evidence of the open nature of these forests in Oklahoma are the labels which have been applied: oak forest, oak openings, scrub oak forest, forest range, forest-prairie ecotone, cross timbers, woodland, pigmy woodland, woodland range, savannah forest, savannah, and chaparral.

Forest studies in adjoining states

Several upland forest investigations have been reported from neighboring states. In Arkansas, Turner (1935) described six upland forest communities, all of which occur in Oklahoma. In a survey of scrub oak forests in the Chautauqua Hills, Kansas, Hale (1955) reported the following percentages of trees: post oak, 56; black oak, 22; and blackjack, 21. He remarked that black oak and blackjack ". . . probably occupy the opposite poles of an ecological gradient in the Chautauqua Hills," since they were never found together. In the Missouri Ozarks, Liming (1942) analyzed 100 blackjack stands. Of the total number of trees, the following percentages were found to occur: blackjack, 52.7; post oak, 16.9 and black oak, 11.5. He remarked that "Natural improvement of the composition of these stands through relatively high mortality of blackjack oak is now progressing rather rapidly. . . ." In discussing the vegetation of Texas, Tharp (1926) indicated that transition from pine-oak to oak forest merely meant a gradual decrease of pine until it had entirely disappeared. He indicated that "Contact with the prairie is generally through an ecotone in which the forest proper gives way at its edge to mottes of timber scattered over grassland." In his study of the western cross timbers of Texas, Dyksterhuis (1948) found that the overstory consisted primarily of post oak (63%) and blackjack (29%), although ten other species were encountered.

---

[1] Contribution of the Oklahoma Biological Survey, Dr. Carl D. Riggs, Director.

Forest studies in Oklahoma

According to Phillips, Gibbs, and Mattoon (1950), "Approximately 10,300,000 acres or about 24% of the State's area is covered with forest growth." In his monograph on the vegetation of Oklahoma, Bruner (1931) reported a well-developed, deciduous forest on the rugged topography of the Ozark Plateau and magnificent forests of towering shortleaf pine in the Ouachita Mountains. Westward, however, he found that "The forest gradually becomes poorer in species and dwarfed in stature, and scrub and grassland become more and more abundant." He reported that blackjack and post oak, in the climax oak-hickory forest, often reached heights of 75 feet whereas they rarely exceeded 40 feet in the oak-hickory savannah. He indicated that blackjack was the dominant tree on dry; exposed hillsides and that post oak occurred in more mesic sites. It was reported also that "Communities dominated by either species alone are infrequent, that is, consocies are not well-developed." In 1943, Duck and Fletcher published a very useful map delineating the game (vegetation) types of Oklahoma, and in 1945 they described these game types more completely. They described five upland forest types and pointed out that the post oak-blackjack oak type included 17,628 square miles with a total area greater than all the other forests (12,253 sq. mi.) in Oklahoma. They encountered this type in 65 of the 77 counties in the state.

Several investigations in Oklahoma have been concerned with limited areas. Little and Olmsted (1931) described the upland forests in the Southeastern Oklahoma Protective Unit. In this report they described a dwarf oak association from the tops of the higher mountains in the northern part of the Ouachitas and an oak-hickory sprouts association which had been caused by severe fires. Eskew (1938) referred to the upland forest of the Wichita Mountains Wildlife Refuge as a mixed oak association with blackjack as the dominant. In 1938, Little described the vegetation of Muskogee County and pointed out that the oak-hickory forest is less luxuriant westward with ". . . crooked, low-spreading trees averaging 25 to 40 feet high and up to 1 foot or more in diameter. . . ." Luckhart and Barclay (1938) described an oak-hickory woodland in the vicinity of Tulsa. They noted that post oak was the dominant but that there were more blackjacks on south-facing slopes. In 1939, Little described a dwarf oak woodland on the upland adjacent to Caddo County Canyons. He indicated that blackjack was the dominant species with eastern red cedar and post oak as important secondary species. In 1947, Barclay reported that post oak was the dominant tree in the upland forest, Bear's Glen, near Tulsa. Dale (1956) stated that woodland communities varied considerably in the Arbuckle Mountains. He observed that post oak and blackjack were always ". . . the most important dominants on the dry, upland soils where the parent materials are granite or porphyry." In preparation for this investigation Rice and Penfound (1955) made a complete census of a blackjack-post oak forest and developed the augmented variable-radius method as the method of choice in sampling the 208 upland forest stands, upon which the current report is based.

General Description

Physical features

Oklahoma is a land of surprising diversity: in geology, in physiography, in topography, in climate. The state slopes southeastward from an elevation of 4,978 feet in the Panhandle to 324 feet in the southeastern corner of the state. The Panhandle and the northwestern corner of the state belong to the Great Plains province (Fenneman, 1938). The Redbed Plains, primarily Permian in age, occupy most of the remainder of the state except the eastern border. Included in the Redbeds Plains region are the Arbuckle Mountains and Wichita Mountains, of Paleozoic age. Superimposed on the Redbeds Plains are many recent dune deposits. The eastern border includes portions of the Ozark Plateaus, Boston Mountains, Arkansas Valley, Ouachita and Gulf Coastal Plain provinces (Fenneman, 1938).

The state of Oklahoma is especially interesting for the study of forest vegetation since it is a border state between the cold temperate north and the warm temperature south and between the arid west and the humid east. It is a state in which the vegetation types, and especially their floral components, are conditioned largely by the north-south cline in temperature and by the east-west gradient in precipitation. The Eastern section is heavily timbered (Figs. 1, 2), the Central section is occupied by savannah-like forest (Fig. 1, 3), and the Western section is primarily grassland, with tongues of upland timber on the sand dunes along the streams and on outcrops of sandstone (Figs. 1, 6).

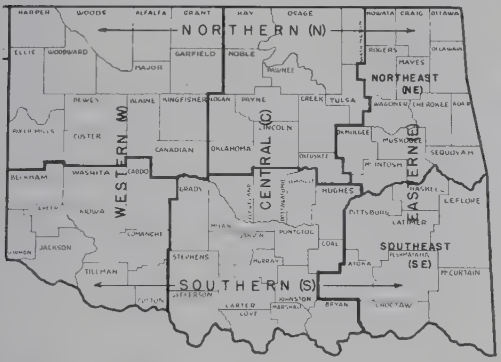

HARPER
WOODS
ALFALFA
GRANT
KAY
OSAGE
NOWATA
CRAIG
OTTAWA
NORTHERN (N)
ELLIS
WOODWARD
GARFIELD
NOBLE
ROGERS
MAYES
MAJOR
PAWNEE
NORTHEAST (NE)
DEWEY
BLAINE
KINGFISHER
LOGAN
PAYNE
CREEK
TULSA
WAGONER
CHEROKEE
ADAIR
WESTERN (W)
CENTRAL (C)
EASTERN (E)
ROGER MILLS
CUSTER
LINCOLN
OKMULGEE
MUSKOGEE
CANADIAN
OKLAHOMA
OKFUSKEE
SEQUOYAH
McINTOSH
BECKHAM
WASHITA
CADDO
GRADY
CLEVELAND
POTTAWATOMIE
SEMINOLE
HUGHES
HASKELL
LEFLORE
GREER
KIOWA
PITTSBURG
LATIMER
McCLAIN
GARVIN
PONTOTOC
COMANCHE
COAL
JACKSON
HARMON
STEPHENS
MURRAY
ATOKA
PUSHMATAHA
SOUTHEAST (SE)
TILLMAN
McCURTAIN
SOUTHERN (S)
COTTON
JEFFERSON
JOHNSTON
CARTER
MARSHALL
LOVE
BRYAN
CHOCTAW

FIG. 1. Sections of Oklahoma referred to in text.

FIG. 2. Extensive oak-hickory-pine forest in southeastern Oklahoma.

Climate

The average annual temperature at Oklahoma City is 60.5° F. However, the mean annual temperature varies from 59.4° F. near Woodward to a mean of 63.7° F. at Idabel in the southeastern corner. The western portion of the state is characterized by greater extremes of temperature than the Central and Eastern sections. The number of days in the average growing season varies from about 200 at Woodward to 240 at Idabel.

The average, annual precipitation varies from about 25 in. at Woodward, in the northwest, to approximately 45 in. at Idabel. Throughout the state, the spring season is the period of greatest rainfall, with summer, autumn, and winter exhibiting decreasing amounts of precipitation, in that order. According to Bruner (1931), the rainfall decreases westward "at the approximate rate of one in. for each twenty miles." Furthermore, the rainfall becomes more torrential westward and less evenly distributed throughout the year. As a result, the conditions are progressively unfavorable for forest development. During the period of our observations (1953 through 1957), the average annual precipitation was 30.25 in. as compared to the normal for that period of 30.70 in. Nevertheless this period constituted one of the worst droughts on record. In 1952 the annual rainfall was only 23.29 in. at Oklahoma City. Inches of precipitaion at Oklahoma City for the actual period of investigation, were as follows: 1953, 31.41; 1954, only 17.84; 1955, 37.42; 1956, only 22.56; and 1957, 42.04. From the above data, it should be noted that the investigation was initiated after a year of subnormal rainfall and that the period of study included two years of very low precipitation. As a result, thousands of native upland trees died, especially in the western part of the state.

FIG. 3. Typical oak-hickory savannah in central Oklahoma, with scattered trees in grassland.

Original forests

The upland deciduous forests of Oklahoma belong to the oak-hickory forest association in the sense of Weaver and Clements (1938). Well-developed oak-hickory forests occur in the Eastern section but are progressively more open westward. According to Marbut (1911), Beilmann and Brenner (1951) and other authors, many of the original arborescent stands were really savannahs, with large trees scattered throughout a grassy landscape. Further evidence of the open, savannah-like nature of many of the original forest stands has been obtained from descriptions of the cross timbers (Foreman, 1947). The name is derived from the fact that these timber belts were disposed across the line of east-west travel of the pioneers (Fig. 6). According to Foreman (1947), "A large part of the cross timbers is included within the counties of Stephens, Grady and Caddo, Oklahoma. . . ." They are composed primarily of blackjack and post oak. Apparently the open nature of these early forests was produced as follows. In the course of a few years the herbaceous vegetation under the trees developed a considerable quantity of litter. When fires started under such conditions all of the seedlings, many of the saplings, and even small trees were destroyed. The result was an open stand of timber, with relatively large trees dispersed throughout a grass-covered terrain (Figs. 3, 4).

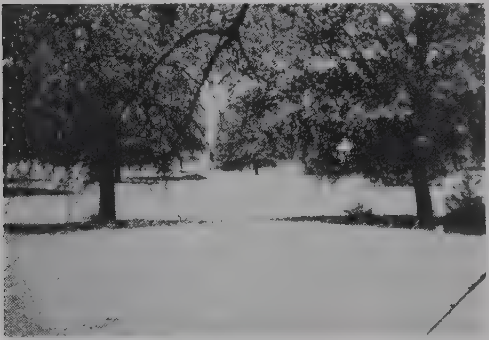


FIG. 4. Heavily grazed oak savannah showing pendant branches of blackjack oak.

Not all of the original stands of timber were savannah-like, however. In many cases, the pioneers literally had to hack their way through the cross timbers, especially in southcentral Oklahoma. Foreman (1947) quotes almost as many travelers as having a difficult time getting through the cross timbers as those who drove wagons through without any trouble. Apparently the answer to the riddle lies in the species of trees which were present. In post oak (*Quercus stellata*)[2] the branches are disposed horizontally and upward whereas in blackjack (*Quercus marilandica*) the tough branches arch downward and remain on the tree for several years after they die (Fig. 4). When blackjack trees are growing in a closed stand, progress, especially with wagons, is incredibly difficult.

Present forests

In the early history of Oklahoma, the forests were reduced drastically by lumbering and by clearing for cultivation. By 1931, Bruner indicated that ". . . All the best and most accessible timber has been cut and to find undisturbed primeval forests one must travel far from the highways." It is probable also that thousands of upland trees in Oklahoma were destroyed by extended droughts in the early thirties and fifties. Many upland trees in Kansas succumbed to desiccation during the dust-bowl days (Albertson 1940, Stiles and Melchers 1935). In Texas, large numbers of trees were killed by the drought of 1949-1954 (Young 1956). On the other hand, there has been considerable invasion of forest trees into areas that were formerly savannah or grassland. This was noted in Arkansas and Missouri by Marbut as early as 1911. In the Missouri Ozarks, Beilmann and Brenner (1951) believed that the encroachment of forests into the ancient prairies had been very rapid, and that our present forests are of relatively recent origin. In Texas also, a pronounced increase of (red cedar) trees into grassland, was observed by Buechner (1944). A considerable extension of forests has taken place in Oklahoma through the production of ravines in grassland by accelerated erosion, and subsequent invasion by trees. Many trees have been planted in cities, around farmsteads, and in shelterbelts. When all of the evidence is examined, it seems probable that there are more trees today than at any other time in the history of Oklahoma.

Bruner (1931) described the following upland forest associations in Oklahoma: *Quercus-Carya* association, *Pinus echinata* consocies, and *Quercus-Carya* savannah. According to Duck and Fletcher (1945) the upland forests of Oklahoma comprise the following types: loblolly pine, oak-pine, oak-hickory, and post oak-blackjack. According to both authors the post oak-blackjack forest (*Quercus-Carya* savannah) extended westward almost to the border of the main body of the state where it gave way to shinnery (Fig. 5). This shrubby community, which does include some trees, occurs mainly in southwestern Woodward, Central Ellis, western Roger Mills, Beckham, and northern Harmon counties. No samples were obtained in this vegetation type because of the shrubby nature of the stands. Duck and Fletcher (1943, 1945) also listed the stabilized dune type for northwestern Oklahoma. This forest type occurs primarily along the north banks of the following rivers: South Canadian, North Canadian, Cimarron, and Salt Fork of the Arkansas. It consists of savannah-like stands of American elm (*Ulmus americana*), western hackberry, (*Celtis reticulata*), and chittamwood (*Bumelia lanuginosa* var. *oblongifolia*). Apparently these trees are the first invaders of the relatively stabilized dunes and are replaced later, at least in part, by blackjack and post oak. No samples were taken in this forest type because of the fragmentary nature of the stands.

---

[2] Nomenclature follows Waterfall's Catalogue of the Flora of Oklahoma (1952) except for several varieties which were not separated in the present report and one variety for which the authority is given in Table X. Common names in Table II.

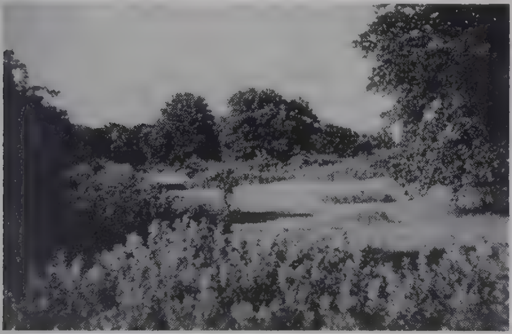


Fig. 5. Contact of oak savannah, shinnery, and grassland in western Oklahoma.

Some of the present upland forests, particularly in the Central and Western sections of Oklahoma, still retain the savannah-like nature of some of the original stands. There is general agreement, however, that the current upland forests possess a greater arborescent cover than the primeval stands. This is especially true in the oak-hickory and oak savannahs. Many heavily grazed and cut-over forest areas have tremendous numbers of saplings and young trees of blackjack and black hickory. Such disturbed stands are so dense that they are virtually impenetrable. According to Dyksterhuis (1957) and according to our own observations and information obtained from early settlers in Oklahoma, heavy grazing and the absence of fire result in the dominance of woody species. It is apparent that these two factors work together to favor trees, shrubs, and woody vines. Heavy grazing weakens the grassland dominants and lowers the fire hazard. Even if fires do get started, they do little damage to the woody components. The result is a continuing increase in arborescent cover and timber volume in areas which were formerly occupied by savannah or grassland. Interdigitation of grassland and oak savannah presents the appearance shown in Figure 6.

In the oak-hickory forest, Oosting (1956) states that "*Quercus alba, Q. rubra, Q. velutina, Q. stellata, Q. marilandica, Carya cordiformis, C. ovata, C. tomentosa* and *C. laciniosa* are species that may be found in the climax anywhere." This is certainly not the case in Oklahoma, although all of the above species were encountered in our study except *C. laciniosa*. Of the above species *Quercus marilandica, Q. stellata, Q. velutina, Carya tomentosa,* and *C. cordiformis* were found in central Oklahoma and only the first two of these were sampled in the western part of the state.

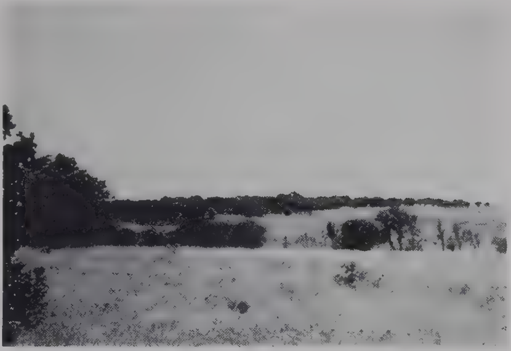


Fig. 6. Interdigitation of oak savannah and prairie in central Oklahoma.

Methods

Field methods

The selection of stands of upland forests in Oklahoma was accomplished according to the following pattern. The vegetation type for a given county was determined by the aid of the Game Type Map of Duck and Fletcher (1943). In the field at least three stands per county were selected by means of county road maps, possible undisturbed stands being located by noting areas with few or no roads. Care was taken also to locate these stands with reference to the vegetation types of adjacent counties. Once the stand was decided upon, data concerning it were entered on an appropriate form. These items included the stand number, location (with included map), past history (including cutting, burning, and grazing), a presence list of trees, shrubs, and woody vines and other miscellaneous data.

An augmented variable-radius method was chosen for analysis of the selected stands. This consisted of the variable-radius technique for determining basal area, supplemented by 40 arms-length rectangles of 0.01 acre each for procuring data on frequency and density (Rice and Penfound 1955). In practice, basal area was obtained at 40 evenly spaced points by means of an angle gauge. Frequency and density were determined by 40 arms-length rectangles between these points. In limited stands only 20 or 30 points were uti-

Table I. Average importance percentage (I.P.) of trees in stands where indicated species were the leading dominants. Two hundred and two stands

No of stands	Leading dominant (With highest I.P.)	Q.m.	Q.s.	C.te.	Q.v.	U.a.	C.to.	P.e.	Q.a.
65	Quercus marilandica, Q.m.	*62.8*	22.3	6.9	8.4	0.7	4.7	6.6	3.0
103	Quercus stellata, Q.s.	20.4	*58.7*	8.5	4.1	3.1	6.7	4.7	0.1
7	Carya texana, C.te.	3.8	11.9	*33.2*	15.5	4.0			1.4
9	Quercus velutina, Q.v.	14.0	18.3	7.8	*38.9*				4.7
2	Ulmus alata, U.a.	11.6	20.7	7.9	17.9	*26.3*	8.0		
1	Carya tomentosa, C.to.	2.3	1.4			0.2	*32.6*	11.6	22.9
10	Pinus echinata, P.e.	3.0	22.7			0.7	5.7	*49.2*	4.9
5	White oak, Q.a.	0.7	4.8			0.9	9.5	2.8	*29.8*

lized. Field data on both trees and saplings were entered on appropriate forms for later analysis.

Compilation methods

After the field notes were brought into the laboratory the following data on each species were entered on a prepared form: number of saplings and trees, frequency of trees, and basal area of trees per sample. From these data the following compilations were made for each species: number of saplings and trees per acre, basal area per acre, relative frequency, relative density, relative basal area, and importance percentage. The importance percentage is calculated by adding the relative data on frequency, density, and basal area and dividing by three. It is equivalent to one-third of the importance value or DFD index of Curtis and McIntosh (1951). The importance percentage has the advantage of being directly comparable to relative frequency, relative density, or relative basal area. Dominants were designated as those species having an importance percentage (I.P.) of 25 or more. Further compilations comprised an ordination of dominants with reference to mesophytism, a table of association-segregates or faciations, a list of upland forest communities and their dominants and several compilations on number, basal area, and importance percentages. In addition, presence lists for all woody species and constance percentage tables for important species were compiled for all sections of the state.

The sections of the state utilized in this investigation were patterned after those of Kelting and Penfound (1953). Changes include a transfer of Canadian, Kingfisher, Garfield, and Grant Counties to the Western section and a shift of Tulsa and Washington Counties to the Central section (Fig. 1).

Forest Types

The forest continuum

Of the total number of arborescent taxa (74) encountered in this investigation, the numbers in the various sections were as follows: Western, 25; Central, 46 and Eastern, 65. This increase of species eastward indicated the possibility of a forest continuum. In order to test this possibility the importance percentages were calculated for each dominant species. Then the stands were arranged into groups, each dominated by one of the eight major species, according to the method of Curtis and McIntosh (1951), but with the xeric stands at the top. When this was done each taxon reached its optimum development at a given point along the series. However, no group of species achieved their peaks in the same stands, and *Quercus stellata* and *Q. marilandica* were fairly prominent in most stands (Table I). Thus no discrete communities could be delineated on the basis of the leading dominants in the stands. This demonstrates that the upland forests of Oklahoma form a vegetational continuum in which a definite gradient is exhibited from the relatively xeric stands to the more mesic stands (Table I).

In discussing the question of the relation of the continuum to the classification of plant communities, Oosting (1956) states that "This leads to the question of the propriety of grouping these communities into units of any system of classification, the argument being that such discrete units do not exist and that it is improper to set up a system with categories whose limits are arbitrarily set. . . ." Despite the obvious fact that the upland forests of Oklahoma do constitute a vegetational continuum, it is relatively easy in the field to recognize distinct stands. Furthermore, at the ends of the continuum an almost completely different group of species is present, e.g. shin oak or western walnut stands in the Western section as against shortleaf pine or loblolly pine communities in the Eastern section. It has, therefore, seemed desirable to sub-divide the oak-hickory forest association into association-segregates or faciations.

Faciations

According to Oosting (1956), "A geographical variant with two or more, but less than the total number, of associational dominants is termed a faciation." Using this definition we have divided the oak-hickory association in Oklahoma into five faciations: oak-loblolly pine, oak-hickory-pine, oak-hickory forest, oak-hickory savannah, and oak savannah (Table II). Since each of these faciations includes several stands or concrete communities, perhaps they should be designated as community-types as recommended by Whittaker (1956). Except for the oak-loblolly pine faciation, the number of dominants decreased westward.

TABLE II. Dominants in upland forest communities of Oklahoma. Species arranged in order of increasing mesophytism (top to bottom). Communities arranged from west to east (left to right)

Species	Oak savannah	Oak-hickory savannah	Oak-hickory forest	Oak-hickory-pine	Oak-loblolly pine
Quercus Havardi (Shin oak)	x				
Juniperus virginiana (Red cedar)	x				
Quercus marilandica (Blackjack)	x	x	x		
Quercus stellata (Post oak)	x	x	x	x	x
Juglans microcarpa (Western walnut)	x				
Carya texana (Black hickory)		x	x		
Quercus velutina (Black oak)		x·	x		
Ulmus alata (Winged elm)			x		
Carya tomentosa (Mockernut)			x	x	
Pinus echinata (Shortleaf pine)				x	
Quercus Shumardii (Shumard's oak)			x		
Quercus alba (White oak)			x	x	
Quercus rubra (Northern red oak)				x	
Pinus Taeda (Loblolly pine)					x
Quercus Muhlenbergii (Chinquapin oak)	x		x		
Acer saccharum (Sugar maple)			x		

Only four dominants were present in the oak-hickory savannah (Table II). Typically only two dominants, post oak and blackjack, were present in the oak savannah, although shin oak, red cedar and western walnut were dominant or codominant in three stands (Table III).

The sixteen species listed as dominants were so designated only if they exhibited an importance percentage of 25 or above in at least one stand (Table II). When they were arranged into groups according to the method of Curtis and McIntosh (1951) a reasonable ordination according to increasing mesophytism was accomplished (Table II). This scheme was supplemented by observing which groups of dominants occurred most often together. When this was done a more satisfactory arrangement was achieved. Since several species were dominant in only one or two stands, however, the position of certain species should be regarded as tentative. This group includes western walnut, winged elm, mockernut and loblolly pine.

TABLE III. Upland forest communities in Oklahoma, arranged in approximate order of increasing mesophytism (top to bottom)

Type of stand	NUMBER OF STANDS			
	Western	Central	Eastern	Total
Shin oak	1			1
Blackjack-red cedar	1			1
Western walnut	1			1
Blackjack-post oak	10	42	19	71
Blackjack	16	7	6	29
Post oak	6	25	21	52
Blackjack-black oak			6	6
Post oak-black hickory		3	3	6
Post oak-black oak		2	3	5
Black hickory-black oak		2	4	6
Black hickory			2	2
Black oak		1	3	4
Winged elm			1	1
Winged elm-post oak			1	1
Mockernut			1	1
Shortleaf pine			5	5
Shortleaf pine-post oak			5	5
Shortleaf pine-white oak			1	1
Shortleaf pine-red oak			1	1
Loblolly pine			1	1
White oak-black oak			1	1
White oak-Shumard's oak			1	1
White oak			4	4
Chinquapin oak	1			1
Chinquapin oak-maple			1	1
Total stands	36	82	90	208

Type of stands

Each of the above faciations includes several types of stands or concrete communities. The oak savannah, which is characteristic of the Western section of Oklahoma (Fig. 4) includes seven different types of stands (Table III). These stands are comparable to the forest cover types of the Society of American Foresters (1932). Each is a distinct community which would be designated as associations by Braun-Blanquet (1932). The more xeric communities included shin oak and red cedar whereas the most mesic community was the chinquapin oak stand on a north-facing slope in the Wichita Mountains. The only really important species in the Western section were blackjack and post oak, since they were dominant in 33 of the 36 stands sampled. It should be emphasized that blackjack and post oak occur as sole dominants in many stands and may contribute 90 per cent or more of the total arborescent cover. This is not in agreement with the statement of Bruner (1931) that "Communities dominated by either species above are infrequent, that is, consocies are not well developed."

The oak-hickory savannah is characteristic of the Central section of the state (Fig. 3). This faciation comprises only four dominant species but several combinations of dominants are represented, as well as numerous single-dominant stands (Table III). As is quite apparent, blackjack and post oak are the principal species, being dominant in 79 of the 82 stands.

The Eastern section of the state comprises all faciations of the oak-hickory forest association in Oklahoma and an extended list of dominants (Table III). The oak savannah and oak-hickory savannah are confined to less favorable sites such as south-facing slopes and ridge tops. The oak-hickory forest is characteristic of the better sites, especially in the Northeast section; the oak-hickory-pine subclimax is more abundant in southeastern Oklahoma; and the oak-loblolly pine faciation is limited to the Gulf Coastal Plain in the southeast corner of the state. In the Eastern section, 21 aborescent communities and 12 dominant tree species were encountered. Of these species, blackjack or post oak was dominant in 64 of the 90 stands sampled. It should be observed, however, that these 2 species were less important, relatively, in the Eastern section, than they were in the Western and Central sections.

Comment should be made here about the arbitrary policy of designating dominants as those species having an importance percentage of 25 or above. When this was done, all stands had one or 2 dominants, except for 3 stands with none and 3 stands which had 3 dominants each. In such cases the stands were designated by the 2 species having the highest importance percentages. In the Eastern section there were 4 white oak stands and one white oak-Shumard's oak community. Usually these 2 species occur together on north-facing slopes and form a distinctive aggregation. In the 5 stands listed, white oak exhibited an average I.P. of 29.5 and Shumard's oak had a mean I.P. of 18.4. Since the average importance percentages of the 2 species were similar, it might appear more logical to include all 5 stands as white oak-Shumard's oak communities. These facts indicate the difficulty that is faced when an inflexible system of classification is utilized. On the other hand, even greater problems are encountered if a more subjective system is employed.

When all types of stands and all sections of the state are considered, blackjack and post oak are the only really important species. Either blackjack or post oak was dominant in 9 of the 25 types of stands. Even more important was the ascendancy of one or the other of these species in 176 of the 208 stands sampled (Table III). Only blackjack and post oak were found to be dominant in every section of the state. Next in importance were black hickory and black oak. These species do not occur in the Western section although they may be prominent in both the Central and Eastern sections. Black hickory or black oak was found to be dominant in seven out of the 25 types of stands and in 29 out of the 208 stands encountered (Table III). Although the remaining species were dominant in 16 out of the 25 types of stands they were prominent in only 27 of the 208 stands investigated (Table III). As a group, therefore, they were of minor importance in the upland forest types of Oklahoma.

DOMINANTS

Number of trees

The number of trees per sample, or per acre, did not vary greatly in the various sections of the state, although a somewhat greater number occurred in the Central section (Table IV). For the state as a whole, the average number was 166 trees per acre, a figure similar to values reported for the oak-hickory forest association elsewhere. The number of saplings (one to three inches DBH) was found to be surprisingly high in all sections of the state (Table IV). Furthermore, saplings of the dominant species were found in every type of community throughout the state. This signifies that all communities were reproducing themselves adequately. This was notably true for the blackjack-post oak forest. For individual stands the range was 0 to 840 saplings per acre, but the average amplitude per section was similar to that given in Table IV. These findings do not agree with the statements of various authors that oak-hickory forests do not reproduce themselves satisfactorily.

TABLE IV. Number of saplings and trees per acre, and basal area in square feet per acre, in upland forests of Oklahoma

	Western	Central	Eastern	Northern	Southern	State
Saplings..	188	207	203	184	218	202
Trees....	166	181	152	159	173	166
Basal area	36.0	48.6	55.3	47.3	51.1	49.2

According to Weaver and Clements (1938) the Cross Timbers ". . . have usually been regarded as portions of the oak-hickory forest . . . They are composed almost wholly of post oak and blackjack . . . which are usually not true climax dominants . . . In this prairie climate, the oaks constitute a post climax, since the climax forest would return in the event of a shift to a wetter climate." As far as climate in Oklahoma is concerned, the blackjack-post oak forest occurs in areas with precipitation ranging from 25 to 45 inches. Typically it occurs on the better sites (usually stabilized sand dunes) in the western part of its range and on the poorer sites (south-facing slopes and ridge tops) in the eastern part of its spread. In general, it is separated from the main body of the oak-hickory forest by the oak-hickory savannah, which comprises black oak and black hickory in addition to blackjack and post oak. With increased grazing and protection from fire, the above savannahs are rapidly returning to forest stature. In view of the above facts it is our belief that the oak savannah and oak-hickory savannah are portions of the oak-hickory forest and that their major components should be regarded as climax dominants.

Basal area

The average basal area of the upland forests of Oklahoma was 49.2 square feet per acre. This is much lower than that of good upland timber stands to the east of Oklahoma. Basal area, in square feet per acre, was very low in the Western section, low in the Central section, and only moderate in the Eastern section (Table IV). There was no significant difference between the Northern and Southern sections in this respect. The absolute range in basal area per stand, in square feet per acre, varied from 7.0 in Western Oklahoma to 115.0 in the Eastern section. Typical ranges in basal area, in the various sections, were as follows: Western, 15-40; Central, 30-60; Eastern, 45-75 (Fig. 7).

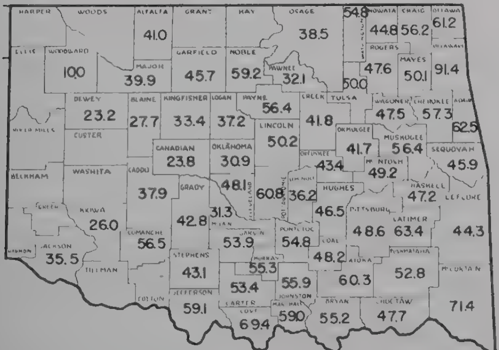

HARPER
WOODS
ALFALFA
41.0
GRANT
KAY
OSAGE
38.5
54.8
NOWATA
44.8
CRAIG
56.2
OTTAWA
61.2
ELLIS
WOODWARD
10.0
MAJOR
39.9
GARFIELD
45.7
NOBLE
59.2
PAWNEE
32.1
50.0
ROGERS
47.6
MAYES
50.1
91.4
DEWEY
23.2
BLAINE
27.7
KINGFISHER
33.4
LOGAN
37.2
PAYNE
56.4
CREEK
41.8
TULSA
WAGONER
47.5
CHEROKEE
57.3
62.5
ROGER MILLS
CUSTER
LINCOLN
50.2
OKMULGEE
41.7
MUSKOGEE
56.4
SEQUOYAH
45.9
CANADIAN
23.8
OKLAHOMA
30.9
43.4
MC INTOSH
49.2
BECKHAM
WASHITA
CADDO
37.9
GRADY
48.1
CLEVELAND
60.8
POTTAWATOMIE
SEMINOLE
36.2
HUGHES
HASKELL
47.2
LEFLORE
GREER
KIOWA
26.0
31.3
42.8
MC CLAIN
46.5
PITTSBURG
LATIMER
48.6
63.4
44.3
HARMON
JACKSON
35.5
COMANCHE
56.5
GARVIN
53.9
PONTOTOC
54.8
COAL
48.2
STEPHENS
43.1
MURRAY
55.3
ATOKA
PUSHMATAHA
TILLMAN
53.4
55.9
60.3
52.8
MC CURTAIN
COTTON
JEFFERSON
59.1
CARTER
LOVE
69.4
JOHNSTON
MARSHALL
59.0
BRYAN
55.2
CHOCTAW
47.7
71.4

FIG. 7. Average basal area of all species combined, in square feet per acre, in counties of the state.

It will be observed that there is considerable variation in basal area, even in adjacent counties (Fig. 7). This is a reflection of the kinds of stands available for sampling as well as the variation in habitat types. In the southwestern corner of the state, for example, the average basal area is relatively low, whereas that in Comanche County is above the average for the state (Fig. 7). This is due to the fact that two of the stands on favorable sites had very high basal areas. As expected, the lowest average basal areas per county were encountered in the Western section, and especially in the northwestern corner of the state. The average basal area per county increased gradually to the eastern border (Fig. 7). The highest volume was observed in Delaware County, where the basal areas, per stand, were 84.75, 115.00, and 74.55 square feet per acre, respectively. In general, the basal area was highest in the Northeast section, which was adjudged to be the most mesic section of the state.

Of the average basal area per acre (49.2), eight species contributed 90.3 per cent. Major contributions were by post oak (40.8%) and blackjack (26.8%). Together, these two species accounted for 67.6 per cent of the total basal area (Table V). By comparison, all other species were minor components, with black oak and black hickory being the most prominent. The second division included shortleaf pine, mockernut, winged elm and white oak, none of which contributed significantly to the total basal area.

TABLE V. Relative basal area and average importance percentage per stand. Arranged according to decreasing importance percentages

Species	Relative Basal Area	Importance Percentage
Post oak	40.8	39.1
Blackjack	26.8	30.5
Black oak	8.1	6.5
Black hickory	4.9	6.4
Shortleaf pine	4.5	3.7
Mockernut	1.8	1.9
Winged elm	1.2	1.9
White oak	2.2	1.7
Other species	9.7	8.3
Total	100.0	100.0

The relative prominence, as indicated by basal area, is portrayed graphically in the following figures (Figs. 8, 9, 10, 11). Attention is called to the fact that post oak is more prominent in the Central section whereas blackjack is more impressive in the Western section. All the other dominants were confined to the Central and Eastern sections but augmented the total basal area only slightly (Figs. 8, 9). When the Northern and Southern sections are considered, it will be observed that post oak exhibited a higher basal area in the Southern division, whereas blackjack was more prominent in the Northern section (Fig. 10). Black oak, black hickory, and white oak also possessed a higher basal area in the Northern section. All of the other dominants were more prominent in the Southern section (Figs. 10, 11).

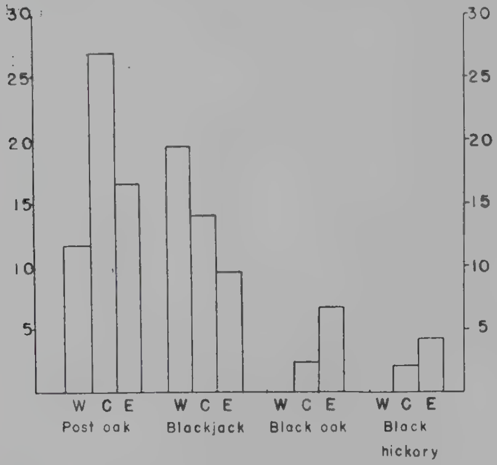


FIG. 8. Average basal area, in square feet per acre, of four leading dominants in Western (W), Central (C), and Eastern (E) sections of Oklahoma.

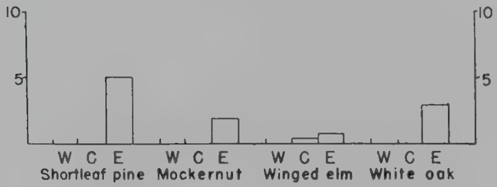


FIG. 9. Average basal area, in square feet per acre, of minor dominants in Western (W), Central (C), and Eastern (E) sections of the state.

The basal area, in square feet per acre, was also determined for the eight leading dominants in each county of the state. Reference to the basal area data on post oak (Fig. 12) indicates that this species was relatively unimportant in the counties of the northwestern portion of the state, whereas it was impressive in the southwestern corner. Blackjack, on the other hand, was more prominent in the northwestern corner, but subordinate in the southwestern portion (Fig. 13). The basal area values, for both post oak and blackjack, were highest in the Central section but decreased eastward, presumably due to competition with the more mesic species of eastern Oklahoma.

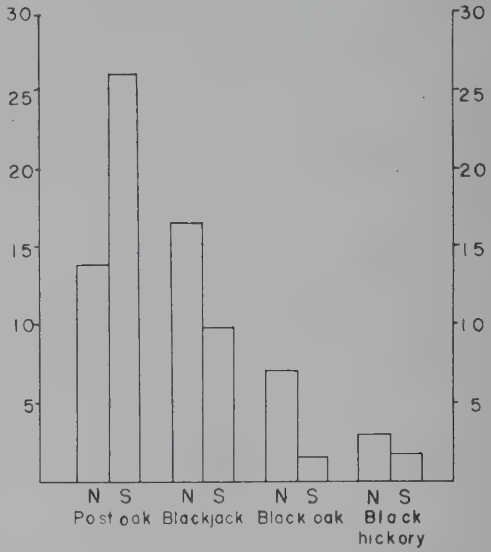


FIG. 10. Average basal area, in square feet per acre, of four leading dominants in the Northern (N) and Southern (S) sections of the state.

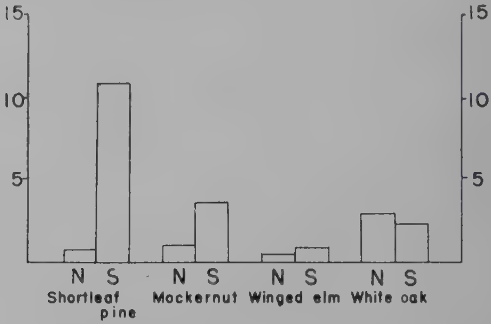


FIG. 11. Average basal area, in square feet per acre, of minor dominants in the Northern (N) and Southern (S) sections of Oklahoma.

It should be noted that the basal area of post oak was about twice that of blackjack in the Eastern section, which suggests that post oak is a better competitor than blackjack (Figs. 12, 13).

Of the next pair of dominants, black oak was relatively prominent in the counties of the Northeastern subsection whereas black hickory was evenly distributed throughout the counties of the Central and Eastern sections (Figs. 14, 15). In many counties of Eastern Oklahoma black oak exceeded both post oak and blackjack in volume (Figs. 12, 13, 14). The second quartet of dominants (shortleaf pine, mockernut, winged elm and white oak) was sampled primarily in the Eastern section. As a group they contributed only a small

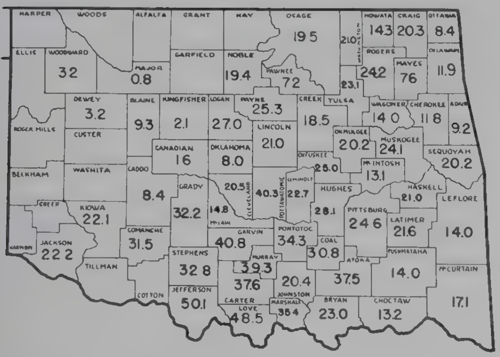

HARPER
WOODS
ALFALFA
GRANT
KAY
OSAGE
19.5
21.0
WASHINGTON
NOWATA
CRAIG
OTTAWA
14.3
20.3
8.4
ELLIS
WOODWARD
3.2
MAJOR
0.8
GARFIELD
NOBLE
19.4
PAWNEE
7.2
ROGERS
24.2
MAYES
7.6
DELAWARE
11.9
23.1
DEWEY
3.2
BLAINE
KINGFISHER
LOGAN
PAYNE
25.3
CREEK
TULSA
WAGONER
CHEROKEE
ADAIR
ROGER MILLS
CUSTER
9.3
2.1
27.0
LINCOLN
18.5
14.0
11.8
9.2
CANADIAN
1.6
OKLAHOMA
8.0
21.0
OKMULGEE
20.2
MUSKOGEE
24.1
SEQUOYAH
20.2
OKFUSKEE
26.0
McINTOSH
13.1
BECKHAM
WASHITA
CADDO
GRADY
20.5
CLEVELAND
40.3
SEMINOLE
POTTAWATOMIE
22.7
HUGHES
HASKELL
21.0
LEFLORE
8.4
GREER
KIOWA
22.1
32.2
14.8
McCLAIN
28.1
PITTSBURG
24.6
LATIMER
21.6
14.0
HARMON
JACKSON
22.2
COMANCHE
31.5
GARVIN
40.8
PONTOTOC
34.3
COAL
30.8
ATOKA
PUSHMATAHA
TILLMAN
STEPHENS
32.8
MURRAY
39.3
37.6
20.4
37.5
14.0
McCURTAIN
COTTON
JEFFERSON
50.1
CARTER
LOVE
48.5
JOHNSTON
MARSHALL
35.4
BRYAN
23.0
CHOCTAW
13.2
17.1

FIG. 12. Average basal area per county, in square feet per acre of post oak.

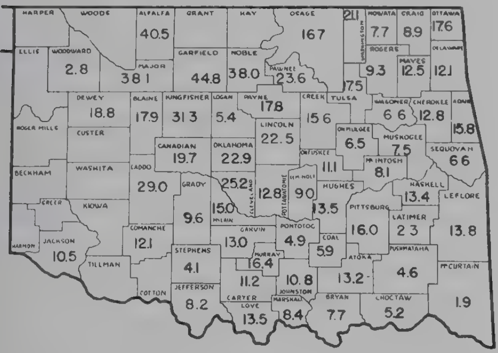

40.5
16.7
21.1
7.7
8.9
17.6
2.8
38.1
44.8
38.0
23.6
9.3
12.5
12.1
17.5
18.8
17.9
31.3
5.4
17.8
15.6
6.6
12.8
15.8
22.5
19.7
22.9
6.5
7.5
6.6
11.1
8.1
29.0
25.2
12.8
9.0
13.4
9.6
15.0
13.5
16.0
2.3
13.8
12.1
13.0
4.9
5.9
10.5
4.1
16.4
4.6
11.2
10.8
13.2
8.2
1.9
13.5
8.4
7.7
5.2

FIG. 13. Average basal area per county, in square feet per acre, of blackjack oak.

percentage (9.7) of the total basal area. Of these species, shortleaf pine contributed the greatest basal area (4.5%), although it was sampled largely in the counties of the Southeastern subsection.

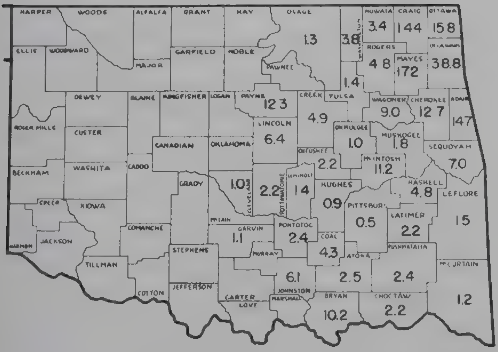

1.3
3.8
3.4
14.4
15.8
4.8
17.2
38.8
1.4
12.3
4.9
9.0
12.7
14.7
6.4
1.0
1.8
2.2
11.2
7.0
1.0
2.2
1.4
0.9
4.8
0.5
2.2
1.5
1.1
2.4
4.3
6.1
2.5
2.4
1.2
10.2
2.2

FIG. 14. Average basal area per county, in square feet per acre, of black oak.

On a collective basis, the other three minor dominants contributed only meager basal area (5.2%), although distributed rather evenly throughout the Eastern section.

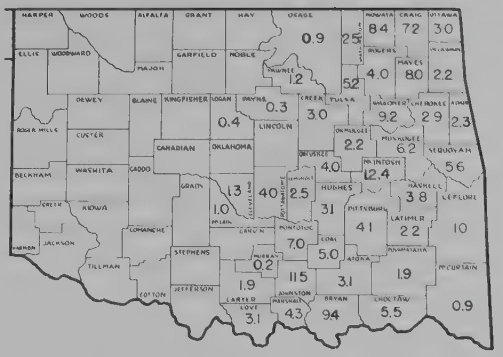

0.9
2.5
8.4
7.2
3.0
1.2
5.2
4.0
8.0
2.2
0.3
3.0
0.4
9.2
2.9
2.3
2.2
6.2
4.0
5.6
12.4
1.3
4.0
2.5
3.8
1.0
3.1
4.1
2.2
10
7.0
5.0
0.2
1.9
1.9
11.5
3.1
1.9
3.1
4.3
9.4
5.5
0.9

FIG. 15. Average basal area per county, in square feet per acre, of black hickory.

Importance percentage

The importance percentage (I.P.) was calculated for all 74 tree species, but the importance percentages for the eight major species only are presented here (Table VI). For the state as a whole, the species may be divided into three groups on the basis of importance percentages: post oak-blackjack, black oak-black hickory, and shortleaf pine-mockernut-winged elm-white oak.

TABLE VI. Average importance percentage per stand in sections of Oklahoma, arranged in order of decreasing importance percentages for the state. Sections: W, Western; C, Central; E, Eastern; N, Northern; S, Southern

Species	W	C	E	N	S	State
Post oak	30.7	52.9	29.8	29.3	48.3	39.1
Blackjack	56.4	32.2	18.5	39.3	22.2	30.5
Black oak		4.3	11.2	9.7	3.5	6.5
Black hickory		6.6	8.8	7.4	5.5	6.4
Shortleaf pine			8.7	0.6	6.8	3.7
Mockernut			4.4	1.0	2.8	1.9
Winged elm		2.0	2.5	1.5	2.3	1.9
White oak			3.9	2.0	1.4	1.7

The post oak-blackjack group had high I.P. values and contribtued 69.6 of the total importance percentage (Table VI). The black oak-black hickory group exhibited moderate I.P. values and accounted for 12.9% of the total. The other four species, mostly eastern in distribution, yielded only 9.2 of the total importance percentage (Table VI).

When post oak and blackjack are compared, it will be observed that post oak had lower I.P. yields in the Western section than blackjack, but higher I.P. values in the Central and Eastern sections (Table VI). On a north-south basis, postoak exhibited higher I.P. values in the Southern section, but lower values in the Northern section, when compared with blackjack (Table VI). Other significant differences on a north-south basis occurred also in black oak, which was very prominent in the Northeastern subsection, and shortleaf pine, which was predominant in the Southeastern subsection (Table VI).

When the relative basal areas and importance percentages are compared, it is evident that they are very similar (Table V). They are almost identical in post oak, whereas the relative basal area is somewhat lower than the importance percentage in blackjack (Table V). This indicates that the DBH was somewhat higher in post oak than in blackjack. This was true also for black oak, shortleaf pine and white oak. The data suggest that either compilation is adequate in determining dominance and importance in the upland forests of Oklahoma.

Effect of Drought

It may be recalled that this investigation occurred during one of the worst droughts on record. Some trees died during the dry summer (17.84 in. of rainfall) of 1954 but widespread death of trees did not occur until 1956 (Fig. 16). Our records, therefore, include the summers of 1956 and 1957 only, and do not comprise many stands, especially in the Central section (Fig. 17). Data were obtained on the death of trees in 79 stands distributed unequally over the state. The results indicate that destruction of trees through desiccation was highest in the Western section, moderate in the Central section, and least in the Eastern section (Table VII).

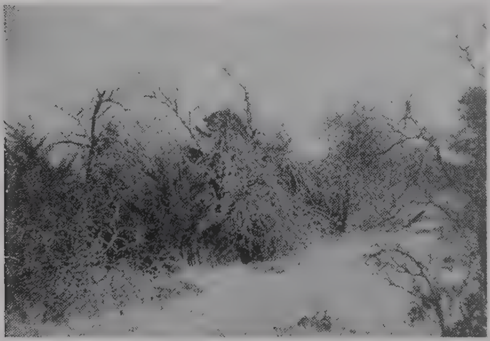


Fig. 16. Death of blackjack trees from drought in oak savannah, western Oklahoma.

The greatest number of trees died in Woodward County in the northwestern corner of the state (42.3%). The number of dead trees in other counties of the Western section was much lower, however (Fig. 17). Destruction of trees by drought in Eastern Oklahoma was much less than in the Western section, no dead trees being encountered in three stands in the Eastern section (Fig. 17). Although our data are meager in the Central section, it seems probable that there was a gradual decrease in number of dead trees from the Western border eastward.

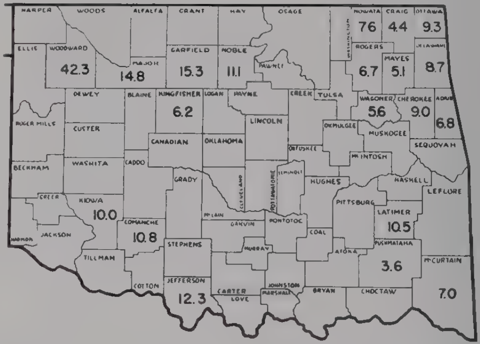

HARPER
WOODS
ALFALFA
GRANT
KAY
OSAGE
NOWATA
CRAIG
OTTAWA
76
4.4
9.3
ELLIS
WOODWARD
42.3
MAJOR
14.8
GARFIELD
15.3
NOBLE
11.1
PAWNEE
WASHINGTON
ROGERS
6.7
MAYES
5.1
DELAWARE
8.7
DEWEY
BLAINE
KINGFISHER
6.2
LOGAN
PAYNE
CREEK
TULSA
WAGONER
5.6
CHEROKEE
9.0
ADAIR
6.8
ROGER MILLS
CUSTER
CANADIAN
OKLAHOMA
LINCOLN
OKMULGEE
MUSKOGEE
OKFUSKEE
SEQUOYAH
BECKHAM
WASHITA
CADDO
GRADY
CLEVELAND
POTTAWATOMIE
SEMINOLE
HUGHES
McINTOSH
HASKELL
LEFLORE
GREER
KIOWA
10.0
McCLAIN
GARVIN
PONTOTOC
PITTSBURG
LATIMER
10.5
HARMON
JACKSON
COMANCHE
10.8
STEPHENS
MURRAY
COAL
ATOKA
PUSHMATAHA
TILLMAN
COTTON
JEFFERSON
12.3
CARTER
LOVE
JOHNSTON
MARSHALL
BRYAN
CHOCTAW
3.6
McCURTAIN
7.0

Fig. 17. Average per cent mortality of trees from drought. From data obtained in 1956 and 1957 only.

Table VII. Per cent dead trees as determined from stands sampled in the summers of 1956 and 1957

Section	No. of stands	Per cent dead trees
Western	13	14.6
Central	11	11.8
Eastern	55	6.6
Northern	48	9.3
Southern	36	10.8

In stands that included both blackjack and post oak, more blackjacks than post oaks were killed by desiccation (Fig. 16). In one stand in Jefferson County 81.5% of all blackjack trees were dead while only 8.5% of the post oak trees were dead. This is contrary to the prevailing opinion that blackjack is the more xeric of these two associates. From the available evidence it appears that blackjack may occur on less favorable sites than post oak but is not as drought-resistant. It seems probable, also, that blackjack has a narrower range of ecological amplitude than post oak.

Status of Savannahs

From the western boundary of the main body of the state eastward, the major vegetation types are as follows: grassland, oak savannah, oak-hickory savannah, oak-hickory forest. It appears that the oak savannah would metamorphose into an oak-hickory savannah in the event of a shift to a wetter climate and that it would change to grassland in the event of a change to a drier climate. This latter shift was almost accomplished in 1956-1957 and would certainly have occurred had the drought continued for a few more years. Similarly, the oak-hickory savannah presumably would be converted into oak-hickory forest with an increase in available moisture and would be transformed into an oak savannah with cumulative desiccation. It should be emphasized that oak savannahs and oak-hickory savannahs occur throughout the main body of the state, with a precipitation range from 25 to 45 in. With the exception of the extreme eastern part of the state, the savannahs occur on soils of fairly course texture derived largely from sandstones or granites. Fine textured soils derived largely from limestones or shales support grassland vegetation. This means that almost all of Oklahoma is a broad ecotone between forest and grassland. Actually, the climate throughout the ecotonal area cannot be said to be either a true grassland or forest climate. The deciding factor is the soil texture, apparently through its effect on water relations.

According to Dyksterhuis (1957) "A savannah type should be regarded as normal, or climax, only on a savannah site." In other words a savannah type should be regarded as climax only in a savannah climate. It seems logical and appropriate to designate the climate in the broad ecotonal zone described above as a savannah climate. In fact, since there are two distinct types of savannah in Oklahoma, it appears logical to postulate two kinds of savannah climates. The oak savannah climax would occur throughout a range of about 25 to 32 inches of rainfall and the oak-hickory savannah climax would extend throughout an area having about 32 to 40 inches of precipitation. Since these savannahs are relatively stable, except during major climatic shifts, and since they are reproducing adequately, it is felt that they should be considered as climax communities and that their major components should be designated as climax dominants.

DISTRIBUTION

Presence

The number of woody taxa encountered in this investigation was 134. This list comprised 74 trees and 60 shrubs and woody vines. Five additional varieties were identified but were not included in the tables because of the difficulty of recognizing these taxa in the vegetative condition. The number of woody species was lowest in the Western section and increased continuously eastward in the state (Table VIII). The number of woody taxa from west to east were as follows: Western, 54; Central, 86; Eastern, 116. Surprisingly, there was a slightly greater number of species in the Northeastern subsection than in the Southeastern portion (Table VIII).

TABLE VIII. Number of woody species per section in the upland forests of Oklahoma based on sampling data. W, Western; C, Central; E, Eastern; NE, Northeastern; SE, Southeastern

	W	C	E	NE	SE	State
Number of stands......	36	82	90	50	40	208
Shrubs and vines	29	40	51	42	37	60
Tree species....	25	46	65	58	52	74

A complete list of trees and their distributions are presented in Table IX. The distribution of several species was extended considerably when herbarium specimens from the Bebb Herbarium, at the University of Oklahoma, were included. In all discussions which follow concerning the restriction of woody species to any section or subsection, data from the herbarium sheets have been included even though all herbarium specimens were not necessarily from upland forests. Distribution data on all woody taxa, including a record of herbarium specimens, were spotted by counties on maps of the state. When this was done, many records for counties were blank where it was felt certain that the species occurred. These maps, therefore, have been omitted, but are available for study at the University of Oklahoma. If, and when, sufficient additional records are obtained, it is hoped that these distributional maps may be included in a later publication.

On the basis of data from samples and herbarium specimens, certain tree species were found to be confined to one section only (Table IX). *Juglans microcarpa* and *Quercus virginiana* were limited to the Western division, no tree species were exclusive to Central Oklahoma, but 15 species were restricted to the Eastern section. *Aesculus glabra* var. *glabra* and *Fraxinus quadrangulata* were confined to the Northeastern subsection, and *Ilex opaca* and *Pinus Taeda* were limited to the Southeastern subdivision. The remaining species (11) occurred in both subsections.

The compilation of total woody species comprised 41 shrubs and 19 vines (Table X). A few species, such as *Menispermum canadense* and *Passiflora lutea,* which are generally essentially herbaceous above ground have been included here as woody vines. As was true for the trees, some were confined to one section, some were limited to two sections, and a few more were present in all three divisions of the state. The following shrubs and vines were present in a very high percentage

TABLE IX. Presence and distribution of tree species in the upland forests of Oklahoma. W, Western section; C, Central; E, Eastern; x, in stands; h, in Bebb herbarium (not always from upland forests)

Taxa	W	C	E
Acer rubrum			x
Acer saccharum	x		x
Aesculus glabra var. glabra			x
Amelanchier arborea		x	x
Bumelia lanuginosa var. oblongifolia	x	x	x
Carpinus caroliniana			x
Carya cordiformis		x	x
Carya illinoensis	h	x	x
Carya ovata		h	x
Carya texana		x	x
Carya tomentosa		x	x
Castanea ozarkensis		h	x
Catalpa speciosa	x	h	h
Celtis laevigata (mostly var. texana)	x	x	x
Celtis occidentalis	h	x	x
Celtis reticulata	x	x	x
Cercis canadensis	x	x	x
Cornus florida	h	x	x
Crataegus crus-galli	x	x	x
Crataegus Marshallii		x	x
Crataegus mollis		x	x
Crataegus Reverchoni var. discolor			x
Crataegus spathulata			x
Crataegus viridis	x	x	x
Diospyros virginiana	h	x	x
Fraxinus americana	h	x	x
Fraxinus pennsylvanica	h	x	x
Fraxinus quadrangulata			x
Gleditsia triacanthos	h	x	x
Gymnocladus dioica	h	x	x
Ilex opaca			x
Juglans microcarpa	x		
Juglans nigra	x	x	x
Juniperus virginiana	x	x	x
Liquidambar Styraciflua		h	x
Maclura pomifera	h	x	x
Morus rubra	x	x	x
Nyssa sylvatica			x
Ostrya virginiana			x
Pinus echinata			x
Pinus Taeda			x
Platanus occidentalis		x	x
Populus deltoides		x	h
Populus Sargentii	x	h	h
Prosopis juliflora var. Torreyana	x	x	h
Prunus mexicana	x	x	x
Prunus serotina		x	x
Quercus alba		h	x
Quercus falcata		h	x
Quercus Harvardi	x	x	
Quercus macrocarpa	h	h	x
Quercus marilandica	x	x	x
Quercus Muhlenbergii	x	x	x
Quercus nigra			x
Quercus palustris		h	x
Quercus Phellos			x
Quercus rubra			x
Quercus Shumardii	x	x	x
Quercus stellata	x	x	x
Quercus velutina		x	x
Quercus virginiana	x		
Rhamnus caroliniana		x	x
Robinia Pseudo-Acacia	h	x	x
Salix caroliniana	x	h	h
Salix nigra	h	x	x
Sapindus Drummondii	x	x	x
Sassafras albidum		x	x
Sophora affinis		x	h
Tilia americana			x
Ulmus alata		x	x
Ulmus americana	x	x	x
Ulmus crassifolia		x	x
Ulmus rubra	x	x	x
Viburnum rufidulum	h	x	x

TABLE X. Presence and distribution of shrubs and woody vines in upland forests of Oklahoma. W, Western section; C, Central; E, Eastern; x, in stands; h, in Bebb herbarium (not always from upland forests)

Taxa	W	C	E
Aesculus glabra var. arguta (Buckl.) Robinson	x	x	h
Amorpha canescens	x	x	x
Amorpha fruticosa	x	x	x
Ampelopsis arborea		x	x
Artemisia filifolia	x	h	
Ascyrum Hypericoides		x	x
Asimina triloba		h	x
Berchemia scandens		x	x
Brunnichia cirrhosa			x
Callicarpa americana		x	x
Campsis radicans		x	x
Ceanothus americanus var. Pitcheri	h	x	x
Ceanothus herbaceus	x	h	x
Celastrus scandens	x	x	x
Cephalanthus occidentalis	x	x	x
Cissus incisa	x	x	x
Clematis versicolor			x
Cocculus carolinus	x	x	x
Cornus Drummondii	x	x	x
Corylus americana			x
Euonymus spp.	h	x	h
Forestiera pubescens var. pubescens	x	h	h
Hypericum densiflorum var. lobcarpum			x
Hypericum frondosum			x
Hypericum spathulatum			x
Ilex decidua		x	x
Ipomoea sp.	h	x	h
Lonicera albiflora	x	h	
Lonicera sp.		x	x
Lyonia ligustrina var. salicifolia			x
Menispermum canadense	h	h	x
Parthenocissus quinquefolia	x	x	x
Passiflora lutea var. glabriflora	h	h	x
Ptelea trifoliata	x	x	h
Prunus angustifolia	x	x	x
Prunus gracilis	x	x	x
Prunus Monsoniana			x
Prunus virginiana	x		
Quercus prinoides	x	x	x
Rhododendron canescens			x
Rhus aromatica var. aromatica	x	x	x
Rhus aromatica var. pilosissima	x	x	h
Rhus copallina var. latifolia	x	x	x
Rhus glabra	x	x	x
Rhus radicans	x	x	x
Ribes odoratum	x	h	x
Rosa carolina var. villosa		x	x
Rosa foliolosa		x	x
Rosa setigera		x	x
Rubus spp.	x	x	x
Sambucus canadensis	h	x	x
Smilax Bona-nox	x	x	x
Smilax rotundifolia	x	x	x
Staphylea trifolia		h	x
Symphoricarpos orbiculatus	x	x	x
Vaccinium arboreum		x	x
Vaccinium stamineum var. neglectum			x
Vitis spp.	x	x	x
Xanthoxylum americanum		x	x
Xanthoxylum Clava-Herculis		x	x

of the stands sampled in every section of the state: *Rhus radicans, R. glabra, Symphoricarpos orbiculatus, Smilax Bona-nox, Parthenocissus quinquefolia,* and *Vitis* spp. Of the shrubs and woody vines, only one species was confined to the Western section and none to the Central section, based on data from samples and herbarium specimens. On the other hand, 10 taxa were limited to the Eastern section.

Constance

Constance percentages were determined for all arborescent species encountered in the study. A comparative compilation of the constance data, on the octette of major species, is presented in Table XI. On a state-wide basis, post oak and blackjack were each present in over 90% of the stands, black oak and black hickory occurred in over 50% of the samples, where the other dominants occurred in a relatively small percentage of the stands. The constance percentages indicate again the wide distribution and prominence of post oak and blackjack in the upland forests of Oklahoma. With reference to constance percentages, both species had the lowest values in the Western section and the highest in the Central division (Table XI). Of all the species, only blackjack was sampled in every stand of a given (Central) section of the state. When compared with post oak, blackjack exhibited a higher constance percentage in the

TABLE XI. Constance percentages of important upland trees in sections of Oklahoma. Arranged according to decreasing importance percentages

Species	Western	Central	Eastern	State
Post oak	69.4	98.7	97.7	93.2
Blackjack	83.3	100.0	93.3	94.2
Black oak		46.3	83.3	54.3
Black hickory		52.4	85.5	57.6
Shortleaf pine			31.1	13.4
Mockernut			67.7	29.3
Winged elm		29.2	45.5	31.2
White oak			27.7	12.0

Western and Central sections but a lower value in the Eastern division (Table XI).

SUMMARY

1. The upland deciduous forests of Oklahoma extend across the main body of the state from east to west with diminishing number and stature of their woody components. Apparently the present upland forests possess a greater arborescent cover than the original stands because of heavy grazing and the absence of fire.

2. This report is concerned with quantitative, phytosociological analyses of 208 stands during the summers of 1953 through 1957.

3. Presence for all woody species was obtained by reconnaissance. The number of trees and saplings was determined by means of 40 arms-length rectangles and the basal area of trees was calculated by an angle gauge at 40 points in each stand. From these data the following compilations were made for each species: number per acre, basal area per acre, relative frequency, relative density, relative basal area, and importance percentage.

4. When dominants were designated as those species having an importance percentage of 25 or above, there were 25 types of stands. Four of these types were confined to the Western section of the state, none was exclusive to the Central region, but 13 types of stands were limited to Eastern Oklahoma.

5. The upland, deciduous forest of Oklahoma was divided into the following faciations or association-segregates: oak-loblolly pine forest, oak-hickory-pine forest, oak-hickory forest, oak-hickory savannah, and oak savannah. The Eastern section comprised all of the above faciations. Except for a few mesic habitats, the Central region included only the last two faciations and the Western section comprised only the oak savannah.

6. On a state-wide basis, the only important tree species were post oak (*Quercus stellata*) and blackjack (*Quercus marilandica*). This was true whether based on presence, constance, frequency, density, basal area, or importance percentage data. Other prominent species, in order of decreasing importance percentages, were black oak (*Quercus velutina*), black hickory (*Carya texana*), shortleaf pine (*Pinus echinata*), mockernut (*Carya tomentosa*), winged elm (*Ulmus alata*), and white oak (*Quercus alba*). Eight other species were dominants in at least one stand.

7. All types of stands were found to be reproducing themselves adequately, as indicated by the abundant saplings present. This was notably true for the stands in the oak-hickory savannah and the oak savannah. These, and other facts, suggest that these savannahs should be designated as climax communities, and that their major components should be considered as climax dominants.

8. Some trees, in every type of community, were destroyed during the extended drought from 1952 through 1956. The greatest destruction occurred in the Western section and the least along the eastern border. In stands that included both blackjack and post oak, more blackjack than post oak trees were killed by the drought.

9. The upland forests of Oklahoma comprised 74 arborescent species and 60 shrubs and woody vines. Several tree species were confined to certain sections of the state, the sections and their exclusive species being as follows: Western, *Juglans microcarpa* and *Quercus virginiana;* Central, none; Eastern, *Pinus echinata, Pinus Taeda* and 14 other species. Of the shrubs and woody vines, only one species was limited to the Western section and none to the Central section. Ten species were confined to the Eastern section.

REFERENCES

Albertson, F. W. 1940. Studies of mature red cedars in west-central Kansas. Kansas Acad. Sci. **43:** 85-95.

Barclay, Harriet G. 1947. The woody vegetation of Bear's Glen, a Washington Irving stopover. Proc. Oklahoma Acad. Sci. **28:** 40-47.

Beilmann, A. P. and L. G. Brenner. 1951. The recent intrusion of forests in the Ozarks. Ann. Missouri Bot. Gard. **38:** 261-282.

Braun, E. Lucy. 1947. Development of the deciduous forests of eastern North America. Ecological Monogr. **17:** 211-219.

———. 1950. Deciduous forests of eastern North America. The Blakiston Co., Philadelphia. xiv + 596.

Braun-Blanquet, J. 1932. Plant sociology, the study of plant communities. (Trans., rev., and ed. by G. D. Fuller and H. S. Conard) McGraw-Hill Book Co., New York. xviii + 439.

Bruner, W. E. 1931. The vegetation of Oklahoma. Ecological Monogr. **1:** 99-188.

Buechner, H. K. 1944. The range vegetation of Kerr County, Texas, in relation to livestock and white-tailed deer. Amer. Midl. Nat. **31:** 697-743.

Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology **32:** 476-496.

Dale, E. E. 1956. A preliminary survey of the flora of the Arbuckle Mountains. Texas Jour. Sci. **8:** 41-73.

Duck, L. G. and J. B. Fletcher. 1943. A game type map of Oklahoma. Oklahoma Game and Fish Dept., Oklahoma City, Okla.

———. 1945. A survey of the game and fur-bearing animals of Oklahoma. Oklahoma Game and Fish. Comm. Bull. **3.** 144 pp.

Dyksterhuis, E. J. 1948. The vegetation of the western cross timbers. Ecological Monogr. **18:** 325-376.

———. 1957. The savannah concept and its use. Ecology **38**: 435-442.

Eskew, C. T. 1938. The flowering plants of the Witchita Mountains Wildlife Refuge. Amer. Midl. Nat. **20**: 695-703.

Fenneman, N. M. 1938. Physiography of eastern United States. McGraw-Hill Book Co., New York. xiii + 714.

Foreman, Carolyn T. 1947. The cross timbers. The Star Printery, Muskogee, Oklahoma. 123 pp. + [8].

Hale, M. E. 1955. A survey of the upland forests in the Chautauqua Hills, Kansas. Trans. Kansas Acad. Sci. **58**: 165-168.

Kelting, R. W. and Wm. T. Penfound. 1953. Literature on the vegetation of Oklahoma. Proc. Oklahoma Acad. Sci. **34**: 126-135.

Liming, F. G. 1942. Blackjack oak in the Missouri Ozarks. Jour. For. **40**: 249-252.

Little, E. L. 1938. The vegetation of Muskogee County, Oklahoma. Amer. Midl. Nat. **19**: 559-572.

———. 1939. The vegetation of the Caddo County canyons, Oklahoma. Ecology **20**: 1-11.

——— **and C. E. Olmsted.** 1931. An ecological study of the Southeastern Oklahoma Protective Unit. 53 pp., Edited by Wm. T. Penfound. Manuscript, University of Oklahoma Library.

Luckhardt, R. L. and H. G. Barclay. 1938. A study of the environment and composition of an oak-hickory woodland in northeastern Oklahoma. Proc. Oklahoma Acad. Sci. **18**: 25-32.

Marbut, C. F. 1911. Soil reconnaissance of the Ozark region of Missouri and Arkansas. U.S.D.A. Bur. Soils Rep't. No. **13**. Pp. 1727-1875.

Oosting, H. J. 1956. The study of plant communities. 2nd ed. W. H. Freeman and Co., San Francisco, Cal. viii + 440.

Phillips, G. R., F. J. Gibbs and W. R. Mattoon. 1950. Forest trees of Oklahoma. 7th ed. Div. For., Oklahoma Planning and Resources Board, Oklahoma City, Okla. 135 pp.

Rice, E. L. and Wm. T. Penfound. 1955. An evaluation of the variable-radius and paired-tree methods in the blackjack-post oak forest. Ecology **36**: 315-320.

Society of American Foresters. 1932. Forest cover types of the Eastern United States. Jour. Forestry **30**: 1-48.

Stiles, E. H. and L. E. Melchers. 1935. The drought of 1934 and its effect on trees in Kansas. Trans. Kansas Acad. Sci. **38**: 107-127.

Tharp, B. C. 1926. Structure of Texas vegetation east of the 98th medidian. Univ. Texas Bull. **2606**. 100 pp.

Turner, L. M. 1935. Notes on forest types of northwestern Arkansas. Amer. Midl. Nat. **16**: 417-421.

Waterfall, U. T. 1952. A catalogue of the flora of Oklahoma. The Research Foundation, Stillwater, Oklahoma. 91 pp.

Weaver, J. E. and F. E. Clements. 1938. Plant ecology, 2nd ed. McGraw-Hill Book Co., New York. xxii + 601.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monogr. **26**: 1-80.

Young, V. A. 1956. The effect of the 1949-1954 drought on the ranges of Texas. Jour. Range Mangt. **9**: 139-142.

PHYTOSOCIOLOGICAL AND ENVIRONMENTAL CHARACTERISTICS OF OUTBREAK AND NON-OUTBREAK AREAS OF THE TWO-YEAR CYCLE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA*[1]

R. F. Shepherd
Forest Zoology Laboratory, Calgary, Alberta

Introduction

In the most severe outbreak areas in the eastern and western parts of North America, the spruce budworm, *Choristoneura fumiferana* (Clem.) (Tortricidae), maintains a one-year life cycle. Within the Canadian Rocky Mountains, however, the budworm's life cycle lasts two years. The outbreaks are also quite different in character. The two-year cycle budworm is present in most of the spruce-fir stands of this region, but high populations recur only in certain restricted stands within this spruce-fir forest. This would indicate that there are essential habitat differences between the outbreak and non-outbreak areas which affect the ability of the budworm to reproduce and survive. Detailed descriptions were made of the soil, plant, and climatic characteristics of these two habitats from a forest community viewpoint. Differences in the environmental conditions between the habitats led to an evaluation of the factors affecting the favorable development of the budworm. The importance of these factors was investigated by assessing budworm survival under the two sets of environmental conditions.

The study areas were located in Banff, Yoho, and Kootenay National Parks in the Canadian Rocky Mountains. Eight outbreak areas were located from past records, and seven non-outbreak areas were selected by the presence of the budworm in suitable host stands where no outbreaks had been reported. These study areas were homogeneous stands of at least four acres. Four of the areas were selected for intensive studies.

---

[1] Contribution No. 484, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada; based on a thesis submitted to the Graduate School of the University of Minnesota in partial fulfillment of the degree of Master of Science, June 1955.

The terms "outbreak" and "non-outbreak" are relative, depending upon population levels between two areas. The budworm can usually be found in either outbreak or non-outbreak areas, but the populations in the former are consistently higher than those in the latter, even in years of generally low abundance. When the macroclimate is favorable for budworm increase, the populations rise in all areas, but much more so in the outbreak areas. During the highest observed populations, the trees in outbreak areas are noticeably defoliated and red tops are quite conspicuous. In the non-outbreak areas many new shoots are defoliated and the budworm is quite common, but extensive defoliation of trees does not take place.

Assistance is gratefully acknowledged to Messrs. B. McPhee, J. K. Robins, A. E. Anderson, and E. F. Thornton for their help in setting up equipment and collecting data; Miss M. Cumming kindly undertook the detection of larval diseases; Mr. D. I. Crossley, formerly of the Canadian Forestry Branch, helped in the soil analysis; and Dr. A. E. Porsild of the Canadian National Museum checked the plant identifications. Special thanks are due to Dr. A. C. Hodson, Dept. of Entomology and Economic Zoology, University of Minnesota, Mr. G. R. Hopping, Officer-in-Charge of the Calgary Forest Zoology Laboratory, and other research officers for advice in the study and for a critical review of the paper.

Life History of the Two-Year Cycle Budworm

The two-year cycle budworm feeds on old and new foliage of Engelmann spruce (*Picea engelmanni* Parry) and alpine fir (*Abies lasiocarpa* (Hook) Nutt.), preferring the new needles of developing buds. A single brood predominates; most adults occur during the even-numbered years with few or none during the odd-numbered years. Greatest defoliation is by late-instar larvae in the even-numbered years. Defoliation in odd-numbered years is usually light enough so that the trees have a chance to recover.

Mathers (1932) first determined the life history of the two-year cycle spruce budworm in British Columbia. This work was repeated by Cook (1953) in the Rocky Mountain area. The eggs are laid towards the end of July and hatch in approximately two weeks. The young larvae do not feed, but spin hibernacula, moult, and overwinter in the second stadium. The next year they feed throughout June as second- and third-instar larvae. Each larva spins a second hibernaculum the first week in July, then moults and overwinters as a fourth-instar larvae. They feed throughout June of the second year as fourth, fifth, and sixth instars and pupate the first week of July. The moths emerge two weeks later.

Forest Type and Density

The spruce-fir stands of this region are mature to overmature climax types, at the end of a sere initiated by fire. Lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) usually follows the fire, and after one to three hundred years the pine is replaced by Engelmann spruce. Shortly after the spruce becomes the dominant tree, alpine fir enters and soon dominates the understory. The large spruce in the overstory are capable of good steady growth for 300 years (Le Barron and Jemison 1953), and often persist for another 150 years before dying. Usually a few remnant lodgpole pine are also present in this upper layer. The fir seldom lives beyond 150 years, but it is capable of seeding and establishing greater numbers of seedlings than the spruce.

Studies in the one-year cycle areas indicated that the danger of stands being damaged by the spruce budworm was related to age and volume of balsam fir, *Abies balsamea* (L.) Mill. (Westveld 1945, Balch 1946). This relationship between forest type and budworm outbreaks was investigated in the two-year cycle area by cruising a half-acre plot in each of the two outbreak and two non-outbreak areas. All trees over one inch DBH were recorded by species and diameter; all trees under one inch DBH were recorded by species and height. Crown cover was estimated using the line intercept method of Lindsey (1955). One thousand feet of transect were laid out and the intercepts of all crowns above breast height were recorded.

A summary of the stand statistics appears in Table I. There is no consistent difference in stand density, or in forest composition as expressed by percentage of fir present. The difference in basal area between outbreak and non-outbreak areas is a result of differences in site factors. A discussion of site will follow later. There is a striking difference in total crown area between outbreak and non-outbreak areas. The former have an average of 59 per cent of the area open, while the latter have 41 per cent of the area open.

Difference in crown cover is important to the

TABLE I. Summary of stand statistics

Plot Number	OUTBREAK		NON-OUTBREAK	
	I	II	III	IV
Basal area/sq. ft./acre	148	133	213	201
No. trees/acre	757	478	1028	608
Per cent fir	81	66	80	62
Per cent crown cover of total area				
—spruce	20	18	35	32
—fir	18	5	24	22
—other (including dead trees)	6	14	1	4
—open	56	63	40	42

TABLE II. Site index of each plot

Plot No.	OUTBREAK AREAS		Plot No.	NON-OUTBREAK AREAS	
	Mean Site Index (ht. in feet at 100 years)	Standard Error		Mean Site Index (ht. in feet at 100 years)	Standard Error
I	64	2.3	III	88	3.3
II	66	3.3	IV	93	2.5
V	59	1.7	VII	92	3.1
VI	74	2 4	X	90	2.7
VIII	66	1.9	XI	74	2.4
IX	56	2.8	XIII	104	5.3
XII	67	2.5	XIV	99	3.6
XV	57	2.8			
Average	63.6		Average	91.4	

ecoclimate of the stand. The more open a stand, the greater the air movement and penetration of radiation and thus the higher the evaporation rates. As will be shown later, this difference in crown cover, through its effect on the ecoclimate, is important to vegetation and to budworm populations.

SITES AND SOILS

Workers in the one-year cycle areas found no relationship between site quality and susceptibility of stands to budworm outbreaks (Jaynes and Speers 1949, Turner 1952). Conversely, the data collected on basal and crown areas indicated that site quality is important in the two-year area. The height and age of ten dominant and co-dominant spruce were measured in each of eight outbreak and seven non-outbreak areas. The ages of ten spruce saplings 4.5 ft. in height from each of the four study plots were used to convert age at breast height to total age. The site indexes were determined by extrapolation to height at 100 years from yield tables for Engelmann spruce (Anonymous 1947). The mean site index and standard error were calculated for each plot and are listed in Table II. They fall into two distinct groups according to outbreak and non-outbreak areas with the non-outbreak areas having considerably higher site indexes.

Soil samples were collected from each horizon. These were air dried and stored in cellophane bags until autumn when the texture and acidity of each sample were determined. For the pH readings the soils were screened, mixed with distilled water, and allowed to stand for twenty-four hours. Three determinations were made with a Beckman pH meter and averaged. Soil moistures *in situ* were determined with Fiberglass Soil Moisture Units and an ohmmeter. Calibration curves were established in the laboratory from sample cores according to standard procedure (Coleman 1950).

Most of the soils are immature. Those of the poorer sites (outbreak areas) are considerably more podzolized with a thin, ash-colored, typical A_2 layer and a conspicuous, red-brown illuvial layer. The duff layer is thin, acidic, and intermeshed with mycelial strands. The soils of the non-outbreak areas are less acidic, with no obvious A_2 layer, but with traces of an A_1 layer. The duff layer, although still a mor, is close to a duff-mull. The substrates of the two areas show no consistent differences; they are usually of silt, sand, fine gravel, or glacial till.

There was considerable seasonal variation in the moisture contents of the soils at the 6-inch level, but at the 30-inch level they were relatively consistent. Approximate values were obtained of the wilting coefficient and field capacity of the soils at the 30-inch depth from Figure 34 of Lutz and Chandler (1946). In the outbreak areas the moisture contents were all close to the wilting coefficient so that moisture was probably limiting at certain periods during the summer. In the non-outbreak areas the percentage of soil moisture was consistently higher than field capacity, resulting in abundant moisture for plant growth at all times.

The studies of site index, soil profiles, and soil moisture all show evidence of a relationship between outbreaks and the site conditions, and indicate that outbreaks are restricted to the drier, poorer sites.

DESCRIPTIONS OF FOREST ASSOCIATIONS

Site differences are often expressed by the plant communities present. Each community develops only under certain habitat conditions, which include all the environmental factors influencing organisms living there. Over a long period of time most of the organisms of the region will, by chance, be given an opportunity to enter the community and, through competition, many of these are eliminated. Thus, by the time climax forests have evolved, the communities which have developed under similar habitat conditions will be almost identical. Descriptions were made of the plant communities in the eight outbreak and seven non-outbreak areas to obtain an indication of their habitats.

The qualitative system of analysis proposed by Braun-Blanquet (1932) was used. The basis of his concept is the forest association which he believes is the fundamental unit of vegetation. Each association is made up of separate stands containing similar combinations of species. The basic distinction between the associations is made through use of fidelity of species for specific associations. That is, the presence of species in only one (predominantly in one) association is used to distinguish between associations. If the plants listed by Braun-Blanquet's system are supplemented with a list of the constant and dominant species, as suggested by Poore (1956), a good vegetative description is obtained.

Estimates were made of the abundance and phytosociological relationships of each species with the aid of scale values. Three characteristics of each plant were estimated: abundance (scale values 0-5), sociability (scale values 1-5), and vitality (scale values 1-4). From these, two other characteristics were derived: constancy (scale values 1-5), and fidelity (scale values 1-5). Representatives of each plant were collected and sent to the National Museum of Canada for confirmation or revision of field identification.

The areas fell into two distinct associations corresponding to outbreak and non-outbreak areas. This would indicate that the habitat conditions, as typified by one association, are conducive to periodically increasing budworm populations, while the conditions in the other association are not.

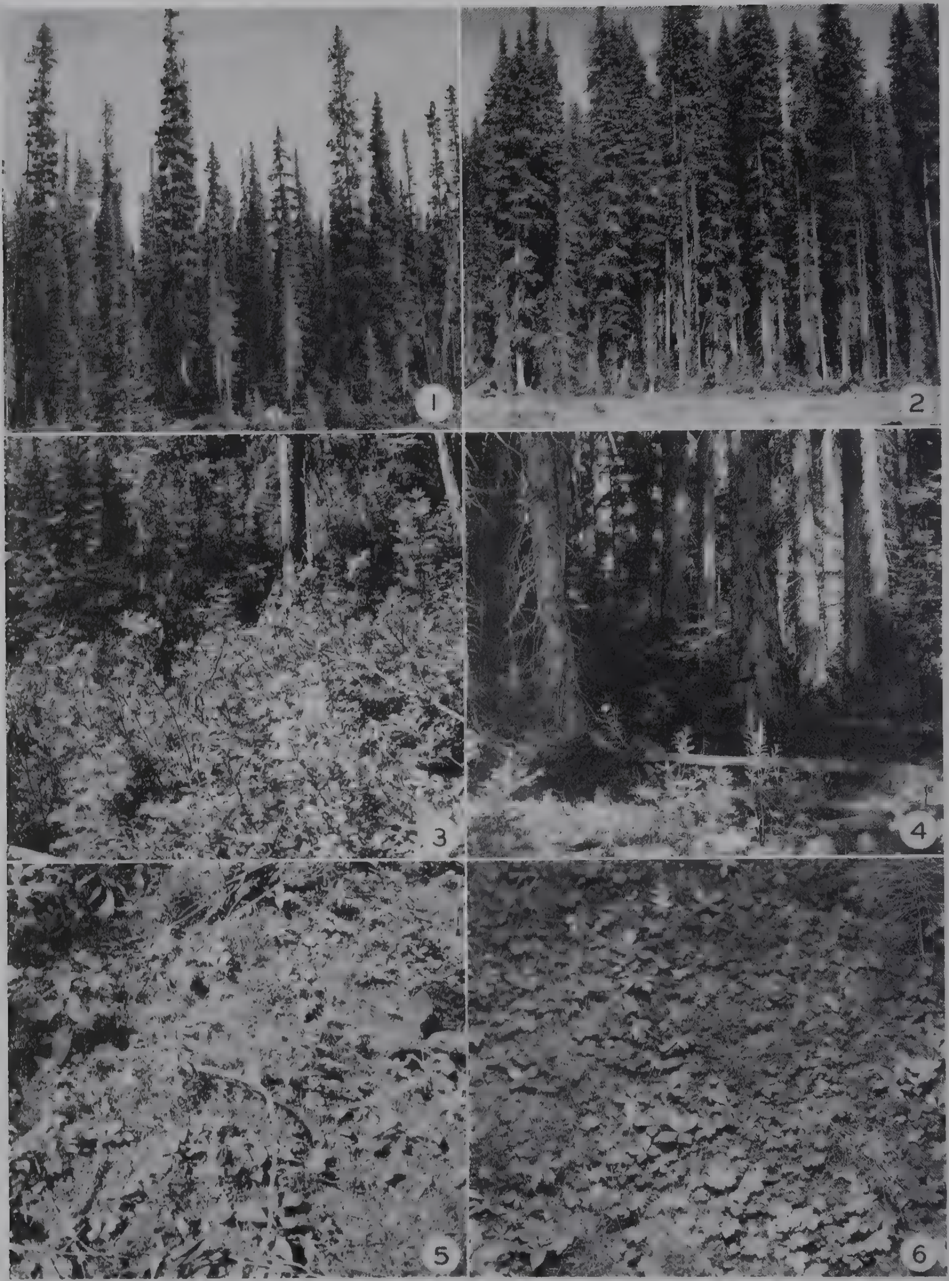
The name proposed for the association which occurs in outbreak areas is *Picea engelmanni-Abies/Peltigera aphthosa* and that for the non-outbreak areas is *Picea engelmanni-Abies/Tiarella unifoliata.* Figures 1 to 6 are comparative photographs of these associations.

The *Peltigera* association occurs on dry sites, usually on steep slopes of the mountains, where drainage is good, the water table deep, and exposure to radiation and drying winds great. The soil is a definite podzol with an acid mor humus and a thin A^2 layer. The red-brown illuvial layers are also quite acidic, and the texture varies from silt to clay loam.

The trees of the overstory are mature to overmature Engelmann spruce with a few residual lodgepole pine and some older alpine fir. The crown conditions are poor; much of the foliage is covered with bearded lichens and shoot growth

TABLE III. Plants of highest indicator value listed by fidelity. Figures refer to average estimates based upon scale values

		Constancy	Abundance	Vitality
	Picea engelmanni—Abies/Peltigera apthosa Association (Outbreak Type)			
Fidelity 5	Exclusive Species			
	None			
Fidelity 4	Selective Species			
	Cladonia gracilis Willd.	3	0.6	3.0
	Ledum glandulosum Nutt.	2	1.5	2.5
	Elymus innovatus Beal.	2	1.5	1.5
Fidelity 3	Preferential Species			
	Peltigera aphthosa Willd.	5	1.3	2.0
	Arnica cordifolia Hook.	5	1.3	2.3
	Menziesia ferruginea Smith var. *glabella* (Gray)	4	3.5	3.1
	Alectoria fremontii Tuck.	3	3.2	4.0
	Dicranum sp. near *scoparium* Hedw.	3	3.0	2.2
	Shepherdia canadensis (L.) Nutt.	3	1.4	3.0
	Juniperus communis L. var. *sibirica* Ait.	3	0.7	2.5
	Pyrola secunda L.	3	0.6	2.7
	Usnea sp.	3	low	2.0
	Empetrum nigrum L.	2	1.0	3.0
	Cladonia sylvatica Hoffm.	1	1.0	2.0
	Picea Engelmanni—Abies/Tiarella unifoliata Association (Non-outbreak Type)			
Fidelity 5	Exclusive Species			
	Tiarella unifoliata Hook.	4	1.6	3.2
	Rubus pedatus Smith.	4	2.1	3.6
	Streptopus amplexifolius (L.) D.C.	4	1.0	3.2
	Equisetum arvense L.	3	3.0	3.5
	Galium triflorum Michx.	3	1.7	3.5
	Dryopteris disjuncta (Ledeb.) C.V. Mort.	3	1.2	2.2
	Petasites palmatus (Ait.) Gray	3	1.0	3.5
	Smilacina racemosa (L.) Desf.	3	low	2.7
Fidelity 4	Selective Species			
	Ribes lacustre (Pers.) Poir.	5	0.8	2.7
	Rubus pubescens Raf.	3	1.3	2.3
	Mitella nuda L.	3	1.0	3.5
	Amelanchier alnifolia Nutt.	3	1.0	1.0
	Clintonia uniflora (Schult.) Kunth.	3	0.6	3.5
	Mnium sp. near *venustum* Mitt.	2	1.0	3.0
	Osmorhiza obtusa (C. & R.) Fern.	1	1.0	4.0
Fidelity 3	Preferential Species			
	Hypnum crista—castrensis Hedw.	5	2.5	3.5
	Lonicera involucrata (Richards.) Banks.	4	1.0	2.5
	Rosa sp.	4	low	0.8
	Thalictrum occidentale A. Gray	3	1.7	3.0
	Vaccinium membranaceum Dougl.	3	1.7	2.7
	Rubus parviflorus Nutt.	3	1.3	2.7
	Scopania sp. near *Blonderi* Aust.	3	0.7	3.5
	Fragaria glauca (S. Wats.) Rydb.	3	0.7	1.2
	Pyrola virens Schweigger	3	low	2.5
	Acer Glabrum Torr. var. *Douglasii* (Hook) Dipp.	3	low	1.3
	Lonicera utahensis Wats.	1	1.0	3.0
	Salix sp.	1	low	1.0



FIGS. 1-6. 1. Edge of a *Peltigera* association. 2. Edge of a *Tiarella* association. 3. Inside a *Peltigera* association. 4. Inside a *Tiarella* association. 5. Typical *Peltigera* association. 6. Typical *Tiarella* association.

is slow with many buds remaining undeveloped. The narrow, ragged crowns provide little protection for the vegetation underneath. The heavy shrub layer is dominated by *Menziesia ferruginea*, but *Shepherdia canadensis* and *Juniperus communis* are also common. The ground is nearly covered by herbs, mosses, liverworts, and lichens. As can be seen in Table III, none of the plants occur exclusively in the *Peltigera* association, and thereforefore no one species is a good indicator. Instead, a combination of plants dominated by *Menziesia* forms a characteristic group which typifies the association.

The association is similar to the one Daubenmire called *Picea engelmanni-Abies/Menziesia ferruginea* in Northern Idaho (1952). The most characteristic shrub is *Menziesia* in both associations. However, the lower herb and moss layers are completely different. In the *Menziesia* association of Idaho the lower layers are quite sparse with only a few species present, and much of the ground is either bare or covered by a thin layer of duff. In contrast to this, the ground of the *Peltigera* association is almost completely covered by plants.

The *Picea engelmanni-Abies/Tiarella unifoliata* association usually occurs in valley bottoms or on wet slopes where there is a high, dependable water table. Exposure is not extreme and the evaporation is comparatively low, so that the drying of the duff layer is not excessive. The soils are not podsolized to the same extent as in the *Peltigera* association. The duff layer is between a mor and a duff-mull, but still acidic. There are traces of an A_1 horizon, but usually the A_2 horizon is absent. The B horizons are slightly acidic and silty loam in texture.

The same species of trees are present as in the *Peltigera* association, but the crowns are full and vigorous. As a result, the protective value of the overstory is much greater. The shrub layer is not so extensive as in the *Peltigera* association; it is made of scattered shrubs of many species. The herb and moss layers contain many species which have a high indicator value such as *Tiarella unifoliata*.

This association is similar to the *Picea engelmanni-Abies/Pachystima Myrsinites* association of Daubenmire (1952). Differences in the shrub, herb, and moss layers separate the two; the most noticeable of these is the deep moist moss layer covering nearly all the area in the *Tiarella* association as compared with a much smaller area of mosses in the *Pachystima* association.

Forest Association Ecoclimates

Forest associations, such as the two described earlier, are the result of differences in the environmental factors. These same factors also affect the animal population and, through their changing influence on mortality and natality rates, may lead to fluctuations of the populations. As climate is one of the most variable of the environmental factors, it probably is a major cause of population fluctuations. The ecoclimates of the two associations were studied with emphasis placed on the factors which would most likely affect the budworm populations.

Evaporation was measured by means of circular copper pans 12 inches in diameter and 6 inches deep, with center posts. At each reading, water was added until the meniscus broke over the point of the central peg. The amount of water added was assumed to equal the evaporation since the last reading. The pans were set 36 inches from the ground; a roof was built above the pans to protect them from radiational heating and rain. Periodic cleaning prevented the accumulation of salts and debris on the surface. Drinking of water by birds was discounted because of the low bird population in the region.

Standard rain gauges were placed 12 inches above the ground in stand openings 20 to 30 feet wide; evaporation and precipitation readings were taken twice weekly. The rainfall showed no consistent differences between outbreak and non-outbreak areas. Hygrothermographs were set up in weather cabinets at standard height in plots I, II, and IV in 1952, in all four plots in 1953, and in plots II and IV in 1954.

The studies described above showed that soil moisture was more abundant in non-outbreak than in outbreak areas. Hygrothermograph charts showed that humidity during the afternoon period was generally lower in outbreak than in non-outbreak areas. The poor protective canopy in the outbreak areas permitted penetration of wind and sunshine. The combined effect of these factors resulted in greater evaporation in the outbreak areas. The evaporation over a four-day period when the weather was clear and sunny, was 0.110 cu. in per sq. in. of surface per day in outbreak areas, and 0.068 in. in non-outbreak areas. In contrast, when the weather was overcast and rainy, there was an evaporation of only 0.021 cu. in. in the outbreak areas and 0.020 cu. in. in the non-outbreak areas.

The total evaporation for the periods of larval activity for the three years of study is given in Table IV. For comparative purposes in this and the next study, the length of the period of larval activity is assumed to be constant (45 days), even though this may have varied somewhat between years and areas. The beginning of the period varied considerably between years, and this has been taken into account in the calculations. Considerable differences in the evaporation rates between the two forest associations are indicated by the data.

TABLE IV. Evaporation during the periods of larval activity of 1952, 1953, and 1954

Plot No.	Total for period in.^{3}/in.^{2} of surface	Average for plots in outbreak or non-outbreak in.^{3}/in.^{2} of surface	% difference* between areas
1952			
I	2.95		
outbreak		3.15	
II	3.35		
			79
III	1.72		
non-outbreak		1.76	
IV	1.80		
1953			
I	2.60		
outbreak		2.69	
II	2.79		
			59
III	1.61		
non-outbreak		1.69	
IV	1.78		
1954			
II outbreak	4.34		
			95
IV non-outbreak	2.73		

$$* \frac{\text{outbreak—non-outbreak} \times 100}{\text{non-outbreak}}$$

As will be brought out later, the difference in evaporation may also influence budworm populations since survival seems to be greatest in the areas with the highest evaporation rates. This relationship between budworm populations and evaporation is based upon work carried out when populations were low. The relationship has been further tested by reconstructing the evaporation rates in the two associations prior to the last budworm outbreak. Precipitation at four local weather stations has been studied; also the annual frequency of cyclonic centers passing over the region has been calculated. These show a decrease in storm centers and precipitation in the period leading to the outbreak. However, such an analysis is too broad to enable close correlation with the type of small local populations that occurred in the two-year cycle areas.

Evaporation is affected by many factors, notably temperature, vapor pressure, wind, and radiation. These factors are interrelated, e.g., during fair weather there are usually high temperatures, low humidity, low winds, and a large amount of radiation. Records of one therefore, are often good indicators of the others. Only a few of these factors are available in the long term weather records, and of these it was believed that maximum temperatures would give the highest correlation to evaporation rates. An attempt was made to determine whether a correlation existed between maximum temperatures and evaporation rates collected from two summers' records in two outbreak and two non-outbreak areas. The evaporation measurements were made twice weekly and this represented the average evaporation for three- or four-day periods. The hygrothermograph charts were checked carefully to select periods when the weather was fairly uniform over these three- or four-day periods and average daily evaporation rates and average maximum temperatures were calculated. The data for the two plots were averaged yielding one set of data for each area. The correlation between the maximum temperatures and the rates of evaporation proved to be exceptionally good in both cases.

The evaporation rates of these areas were then correlated with the maximum temperatures of the closest weather station at Banff, approximately 25 air miles from the study areas. The regression curves are presented in Fig. 7. The regression equations are:

Outbreak area: $\log y + 1 = -0.10564 + 0.00203\,x \;(r = 0.956)$

Non-outbreak area: $\log y + 1 = 0.05368 + 0.00106\,x \;(r = 0.925)$

where y is the daily evaporation rate and x is the maximum temperature.

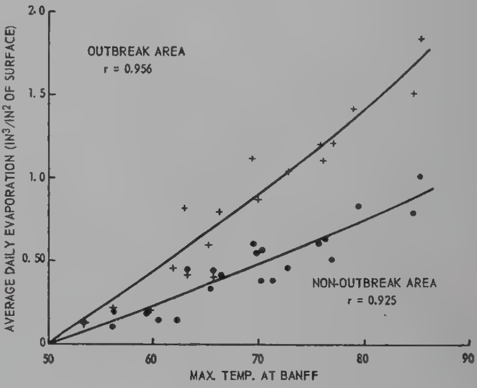


FIG. 7. Regression curve of the average daily evaporation rates in outbreak and non-outbreak areas in Kootenay National Park and the maximum temperature at Banff. Each point represents daily averages based on three- or four-day periods.

Such curves facilitate quick calculation of the evaporation rate from the maximum temperatures which occur in Banff. As these curves were based on average figures, it was still questionable if they would be accurate on a daily basis. The expected evaporation from the curves was compared with the actual evaporation measured on the plots over the 127-day period, May 28 to September 30, 1952. Only half the points (11 representing 38 days) used to establish the curves came from this check period. The calculated evaporation was 2.9 per cent high for outbreak areas, and 1.2 per cent low for non-outbreak areas. As these were within acceptable limits of error, it was concluded that such results should allow the calculation, with a high degree of confidence, of evaporation rates in the study areas for the previous 25 years.

Evaporation was considered to be of major importance during the period of larval activity. The beginning of this period varies considerably from year to year (as much as four weeks). Rose and Blais (1954) showed that abundant larval emergence from overwintering hibernacula took place after maximum temperatures reached 60°F or above. The starting date for the present study was calculated by summing the degree days above 60° F from May 1 to the date of emergence during the years of study. It was found that larval activity began after about 60 degree days. This technique gives only a rough approximation of the commencement of larval activity, but permits better timing of the period for calculating the evaporation rates.

Evaporation rates for the outbreak and non-outbreak areas were estimated from 1928 to 1953 from Banff maximum temperatures. Records were not available for 1946 and 1948 and temperatures from Lake Louise were substituted. New regressions were not calculated for this station so evaporation estimates for these two years are approximate. The evaporation rates of every second year are plotted in Fig. 8, each point representing the period when the larvae of each generation feed openly upon the foliage and are most exposed to the influence of the weather.

Based upon the period 1948 to 1954, it was concluded that evaporation rates above 3.0 cu. in./sq. in. of surface for the last 45 days of larval activity are favorable for budworm increase. Starting in 1934, there were five successive generations of budworm which experienced these high evaporation rates. By the fifth generation, in 1942, budworm populations reached their climax and defoliated large areas of spruce-fir stands. In 1944, populations decreased and defoliation was less obvious. From 1948 to 1950, budworm populations in some restricted areas again increased to a point where defoliation was noticeable, and this increase was again associated with higher evaporation rates. Following 1952, populations declined.

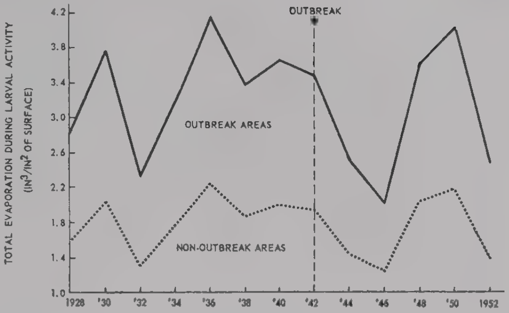


FIG. 8. The evaporation history of outbreak and non-outbreak areas for the period of larval activity, based upon Banff maximum temperatures. Only the even numbered years are plotted, as these are the years when the larvae are more exposed to weather influences.

This indicates that there is a correlation between the rates of evaporation and the fluctuations of budworm populations. In outbreak and non-outbreak areas, populations increased in years of high evaporation and decreased in years of low evaporation. Evaporation rates in the non-outbreak areas never approached the magnitude of the rates in the outbreak areas, and populations never reached a level high enough to cause noticeable defoliation.

PERIODICITY OF ALPINE FIR FLOWERING

The one-year cycle budworm feeds on staminate flowers as well as foliage of balsam fir. Staminate trees provide better food (Blais 1952), a favorable place to live (Wellington 1950a), and a preferred oviposition site (Blais, *op. cit.*). Thus, staminate trees commonly have more and faster developing larvae on them than non-staminate trees. Staminate flowers of alpine fir probably offer the same benefits to the two-year cycle budworm, and differences in this food factor between areas could account for the differences in budworm populations between outbreak and non-outbreak areas.

The relative abundance of staminate flowers over the past twenty years was determined from the flower scars on the branches. Twenty alpine fir trees in an outbreak area and twenty in a non-outbreak area were felled in 1953. The trees were largely co-dominants and were selected as probably supporting the greatest flower production by their size, crown quality, and exposure. From each tree, ten branches which were at least twenty years old were taken from the upper crown. The internodes of each branch were dated by counting back from the terminal bud and the presence or absence of staminate cone scars noted

The variation in flowering during the last twenty years in each area illustrated in Fig. 9. The abscissa has been shifted one year to show the year of flowering instead of the year in which the buds were formed and upon which internode the resulting scars appeared. In the areas studied, defoliation was first noted in 1940 and became the heaviest in 1942. During the pre-outbreak period in this area, there was a steady increase in the amount of flowering up to the peak year of 1941. In the non-outbreak area there was a similar increase up to 1940, but a severe reduction in 1941, the non-flight year previous to heavy defoliation. Nearly twice the flower production occurred in the outbreak areas as in non-outbreak areas.

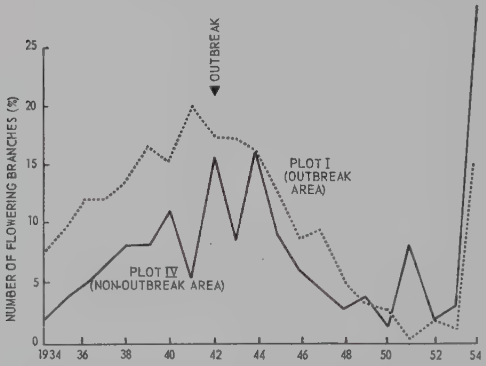


FIG. 9. Graph of the number of branches of alpine fir which bore flowers for each year from 1934 to 1954. The abscissa has been shifted one year to show the year of flowering instead of the year in which the buds were formed and upon which internode the resulting scars appeared.

Although the increase in the amount of flowering of alpine fir before the last outbreak may have aided the rise of budworm populations, the synchronization between areas suggests that the rise in flowering and in budworm populations may be the result of independent responses of both tree and insects to another factor, such as weather, rather than to a dependent relationship between the two. The study of the evaporation in the two forest associations indicates that there was a hot, dry period during the years of increased flowering. An increase in flowering following dry, sunny periods has been cited by a number of investigators. Morris (1948) found that the normal cycle of flower production of balsam fir (*Abies balsamea* (L.) Mill.) is interrupted by additional crops following hot, dry years.

VARIABILITY OF SEASONAL DEVELOPMENT

During the growing season frosts frequently occur in some parts of the region. As seasonal development may differ between outbreak and non-outbreak areas, significant differences in larval mortality from late frosts, or in the co-ordination of larval emergence and foliage production, may appear which could give rise to different population levels between areas. Prebble (1945, 1948) noted a reduction in budworm populations due to frost in the Sault Ste. Marie district. He concluded that the amount of larval mortality was dependent on the time of spring emergence; mortality was greater in years when seasonal development started early in the year.

Differences in the rate of development may also be important to populations in outbreak and non-outbreak areas. Greenbank (1956) found that in years of favorable weather the budworm was able to feed upon early foliage and produced females with greater fecundity. In addition, shorter developmental time reduced the time of exposure to mortality factors.

The length and diameter of terminal shoots on five alpine fir and five Engelmann spruce saplings (3-5 ft.) were measured twice weekly in each of two outbreak and two non-outbreak areas during 1952. The radial increment of five dominant or co-dominant alpine fir trees on each plot were measured at breast height with a dendrometer. When dominant or co-dominant fir was not available, intermediate trees were used.

Collections of larvae were made every seven to ten days on each plot. Where possible, one hundred larvae were hand picked at random from the foliage. These were preserved in 70% alcohol, later separated into instars by head capsule measurements, and dried at 90°F and approximately 2-3% R.H. The larvae were dried to constant weight, then individually weighed with a torsion balance to the closest one-twentieth of a milligram. A total of 1674 larvae were measured for head capsule widths and 1441 were weighed.

Cumulative growth curves were drawn for terminal and radial growth. Little difference in seasonal growth patterns was found between the two species of trees, although the effect of sites previously described was quite distinct. Time of initiation and cessation of growth were similar in all plots except one in a non-outbreak area where a slightly longer growing season occurred because of favorable moisture conditions.

The times of some phenological events for the budworm and the host trees were noted through the season but none showed any important relationships which could be attributed to outbreak or non-outbreak areas. In most cases, the development of one outbreak area was slightly behind that of the other areas.

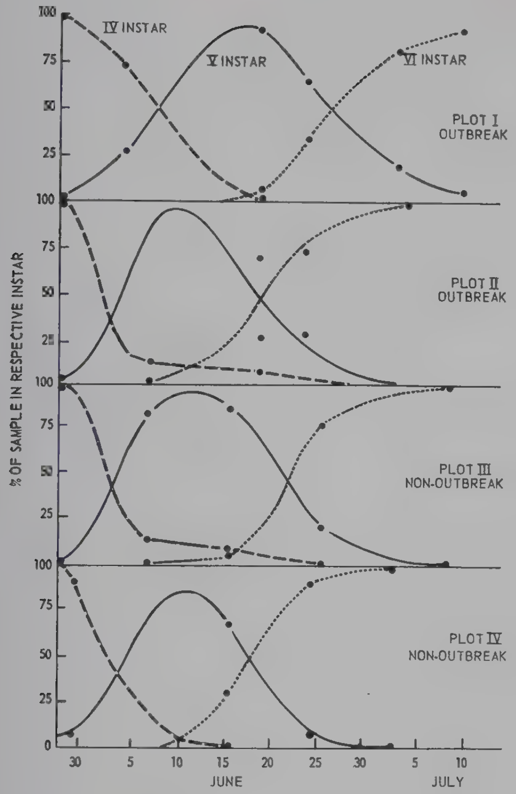


FIG. 10. Curves of the proportion of the population in the respective instars for each plot.

The percentage of the sample in each instar was calculated from head capsule measurements and then plotted according to the time the sample was taken (Fig. 10). Curves were drawn through these points representing the proportion of each instar present at any particular time. Although the larval development differed as much as eight days between the four plots, there seemed to be no consistent relationship between the rate of larval development in outbreak and non-outbreak areas.

The larval developmental rates were also calculated on the basis of body weight. The data on weight were treated with a log (x + 1) transformation which allowed the plotting of regression lines for the various plots. With such a transformation, the assumptions necessary for the derivation of the regression lines and for the application of tests of significance were met. A total of 1441 measurements were used to establish the four lines which appear in Fig. 11. The slope of the line represents the rate of development. These slopes were .0236 and .0283 for the two outbreak areas and .0276 and .0331 for the non-outbreak areas. It is obvious, without any tests of significance, that these developmental rates do not fall into two groups which could account for the restriction of outbreaks to certain areas.

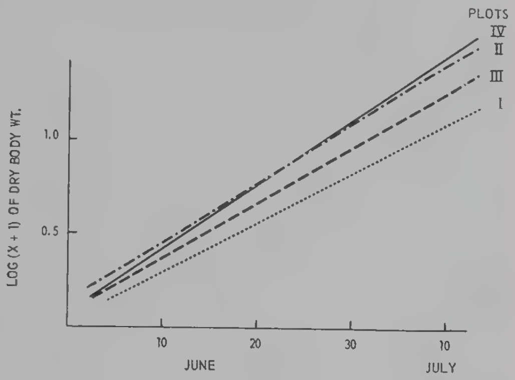


FIG. 11. Log x + 1 transformation of the rate of growth by dry body weight for each plot. Regression lines are plotted by the method of least squares. Plots I and II are outbreak areas and III and IV non-outbreak areas.

As shown in the evaporation study (Fig. 8), 1952 was a wet year in the two-year cycle area. Wet, cold weather tends to equalize the ecoclimates of the different associations, thus largely preventing any differential rate of development of larvae of one association over those of another association. The differences that would occur in development rates during dry years are still unknown.

Hygrothermographs were maintained in the same stands concurrently with the growth and developmental studies for the three years 1952, 1953, and 1954. Highest and lowest minimum temperatures were consistently found in outbreak areas; therefore, late spring frost was discounted as a factor causing population differences between the two areas.

Spruce Budworm Survival

The above sections describe outbreak and non-outbreak areas from the standpoint of forest association, site, ecoclimate, phenology, and forest composition in their relation to budworm incidence. From these descriptions, inferences can be made of the environmental factors affecting budworm survival. Unfortunately, it was not possible to determine survival of natural populations in the areas. Populations were so low that sampling to determine survival at the various stages of the life cycle was not practical. As an alternative, trees were artificially infested in the outbreak and

TABLE VI. Survival and mortality rates for fourth to sixth instar larvae and pupae on artificially infested trees

Mortality or Survival Factor	OUTBREAK				AVE.	NON-OUT-BREAK				AVE.	Probability of a difference between outbreak and non-outbreak areas.
	1954		1956			1954		1956			
	No.	%	No.	%	%	No.	%	No.	%	%	
Fungus Diseases	0	0	2	5.7	2.0	12	9.1	61	45.5	27.5	>.99
Virus Disease	3	4.5	1	2.9	4.0	15	11.4	11	8.2	9.8	.97
Unknown Mortality	4	6.1	17	48.5	20.8	24	18.2	24	17.9	18.0	.54
Survival Adult	59	89.4	15	42.9	73.3	81	61.3	38	28.4	44.7	>.99

non-outbreak areas, and the survival of these populations was observed closely.

Two cages were set up, one in an outbreak area and the other in a non-outbreak area; each cage was 11′ x 8′ x 8′ and covered two fir trees 7 feet high. These cages were covered with overlapping chicken wire to prevent bird predation without seriously affecting either parasitism or climate. A cloth was stapled on a wooden frame covering the area below the trees. Around the edge of this frame a band of tanglefoot was spread to trap any larvae which fell or spun down and wandered to the edge of the tray. Two 1-foot wooden squares covered with tanglefoot were placed on the roof of each cage to check for any larval drop from trees above.

The budworm used to infest these trees came from a third area, 1 mile east of Field, British Columbia. About 700 fourth-instar larvae were placed upon each tree and weekly counts made until adult emergence. All dead larvae on the frame or trees were immediately placed in gelatin capsules and either held for parasitism or sent to the laboratory for disease identification. The latter part of two life cycles was studied on the same trees, introducing new populations each time. Attempts were made to follow the early part of the life cycle from egg to third instar, but these were unsuccessful.

A survey of parasitism was made in 1954 in two outbreak and one non-outbreak area before the above populations were introduced from the field. Populations were too low for mass collections in the other non-outbreak area. Fifth- and sixth-instar larvae were collected and reared until pupation and emergence of either moths or parasites.

The incidence of parasitism found in the areas is presented in Table V. For many years workers in this region have noticed that parasitism of the budworm was low, but no quantitative data had been taken. This survey, based on 2070 budworms taken during a period of decreasing populations, corroborates these observations, so that it is unlikely that parasitism is a primary factor causing the differential rise and fall of budworm populations between outbreak and non-outbreak areas.

TABLE V. Total parasitism appearing in fifth and sixth instar larvae

Area	Per cent parasitism	Number reared
Plot I (Outbreak)	3.09	518
Plot II (Outbreak)	1.85	1135
Plot III (Non-outbreak)	0.24	417
All Areas	1.84	2070

The results of the mortality study of the introduced populations is given in Table VI. Statistically significant differences were found between outbreak and non-outbreak areas in survival, and in mortality due to fungus and virus diseases in both 1954 and 1956. The most important fungus disease was *Beauveria bassiana* (Bals.)

The relationship of the higher incidence of virus infections to the moist ecoclimate of the *Tiarella* association cannot be definitely established, as little is known of the effect of environmental factors on the spread and the infection of diseases caused by virus. It is definitely known, however, that fungus diseases are favored by moist air. Hart and MacLeod (1955) showed that few spores of *Beauveria bassiana* (Bals.) germinated below 94 per cent R.H. With increased humidities there was a corresponding increase in germination.

The average unknown mortality (where no disease or parasitism was present) was similar in both areas. There was, however, considerable difference between years. The unknown mortality during 1954 was 6.1% when calculated evaporation was 3.01, an intermediate year as far as evaporation is concerned (see Fig. 10). In 1956 unknown mortality increased to 48.5% when evaporation was 2.32, an unfavorable year for budworm increase. The same trend of unknown mortality did not follow in non-outbreak areas, but the large number of budworms found infected by fungus diseases may have masked a possible increase in the unknown mortality in 1956.

Observations indicated that at least part of the unknown mortality could be attributed to upset behavior patterns. During wet weather larvae were inactive and did not feed, spin, or moult. When the wet weather persisted many larvae died. This is supported by laboratory behavior studies on the one-year cycle budworm (Wellington 1950b). First-instar larvae spun their hibernacula more rapidly at a high rate of evaporation. If the rate of evaporation fell, the time necessary for spinning increased, and the percentage of larvae able to complete their hibernacula decreased until at saturation the larvae were effectively immobilized. When second-instar larvae left their hibernacula in spring, they moved to their feeding sites in the new buds. Their rate of movement was controlled by the rates of evaporation. These larvae moved fastest at a high rate of evaporation; at lower rates the speed of crawling decreased rapidly. The sixth-instar larvae were also sluggish and slow moving at low rates of evaporation and could only feed, move, and develop properly at higher evaporation rates. It can be seen that larvae which live in a dry habitat, such as the *Picea Engelmanni-Abies/Peltigera aphthosa* association, have an advantage over the larvae exposed to lower evaporation rates of a moist plant community.

Greenbank (1956) has pointed out that not only is the success of the spruce budworm related to climate through mortality, but also through changes in fecundity. Larvae that feed on staminate flowers have increased fecundity, and, as discussed earlier, staminate flower production increases in dry years. In addition, during warm dry springs, larvae that develop faster are able to feed more upon young foliage and this increases fecundity.

The budworm is present in endemic numbers throughout most of the mature spruce-fir stands of the region under study. Usually these populations are quite low and no defoliation is noticeable. These studies indicate that the high mortality which keeps the populations on a low level is at least partially attributable directly and indirectly to the high moisture conditions, or conversely, to low evaporation rates. During dry years, evaporation rates are increased, allowing a greater number of larvae to complete development. These evaporation rates are not only determined by the regional weather systems, but also by the habitats of the various stands. The difference in the evaporation rates between the *Peltigera* and the *Tiarella* association increases with any regional increase in evaporation resulting in a comparatively greater 'release' of the budworm in *Peltigera* association.

It has been estimated that the one-year cycle spruce budworm usually requires four or five years of hot dry weather in June and July to increase to outbreak proportions. In the two-year cycle budworm this period would have to be extended to eight or ten years, but with emphasis on every second year when the larvae are in the sixth instar.

SUMMARY

The spruce budworm of the spruce-fir forests in the Canadian Rocky Mountains maintains a two-year life cycle, overwintering in the second and fourth instars. The life cycles are largely coordinated into one brood so that most adults are found during the even numbered years, i.e., 1954, 1956, 1958. While the budworm usually can be found in most of the stands, populations in certain restricted stands are consistently higher. The latter are called outbreak areas and can be recognized easily by marked defoliation and conspicuous red tops. In the non-outbreak areas the budworm may be quite common, and many new shoots may sometimes be defoliated, but extensive defoliation of the trees does not occur.

REFERENCES

Anonymous. 1947. British Columbia Forest Service Yield Tables. 46 p.

Balch, R. E. 1946. The spruce budworm and forest management in the Maritime Provinces. Canada Dept. Agr., Div. Ent., Proc. Pub. #60 Ottawa. 7 p.

Blais, J. R. 1952. The relationship of the spruce budworm to the flowering condition of balsam fir. Can. Jour. Zool. **30**: 1-29.

Braun-Blanquet, J. (Translated, revised, and edited by G. D. Fuller and H. S. Conard) 1932. Plant Sociology. McGraw-Hill. New York. 439 p.

Colman, E. A. 1950. Manual of instructions for use of the fiberglas soil-moisture instrument. Berkeley Scientific Division of Beckman Instruments Inc. 20 p.

Cook, J. A. 1953. Life history and population studies of the two year cycle spruce budworm *Choristoneura fumiferana* (Clem.) in Banff, Kootenay, and Yoho National Parks of the Rocky Mountains and reference to the forest composition. Master's Thesis, Univ. New Brunswick, Fredericton, N.B. 78 p.

Daubenmire, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecological Monog. **22**: 301-330.

Greenbank, D. O. 1956. Role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. 1. Role of Climate. Can. Jour. Zool. **34**: 453-476.

Hart, M. P., and D. M. MacLeod. 1955. An apparatus for determining the effects of temperature and humidity on germination of fungus spores. Can. Jour. Bot. **33**: 289-292.

Jaynes, H. A., and C. F. Speers. 1949. Biological and ecological studies of the spruce budworm. Jour. Ec. Ent. **42**: 221-225.

LeBarron, R. K., and G. M. Jemison. 1953. Ecology and silviculture of the Engelmann spruce-Alpine fir type. Jour. For. **51**: 349-352.

Lindsey, A. A. 1955. Testing the line-strip method against full tallies in diverse forest types. Ecology **36**: 485-495.

Lutz, H. J., and R. F. Chandler. 1947. Forest Soils. John Wiley. London. 514 p.

Mathers, W. G. 1932. Spruce budworm in B.C. For. Chron. **8**: 154-157.

Morris, R. F. 1948. How old is a balsam tree? For. Chron. **24**: 106-110.

Moss, E. H. 1955. The vegetation of Alberta. Bot. Rev. **21**: 493-567.

Poore, M. E. D. 1956. The use of phytosociological methods in ecological investigations. IV. General discussion of phytosociological problems. Jour. Ecology **44**: 28-49.

Prebble, M. L. 1945. Spruce budworm. Canada Dept. Agr., Div. For. Biol., Bi-monthly Prog. Rept. **1(4)**: 2.

Rose, A. H., and J. R. Blais. 1954. A relation between April and May temperatures and spruce budworm emergence. Can. Ent. **86**: 174-177.

Turner, K. B. 1952. The relation of mortality of balsam fir by the spruce budworm to forest composition in the Algoma forest of Ontario. Can. Dept. Agr., Publ. **875**. 107 p.

Wellington, W. G. 1950a. Effects of radiation on the temperature of insectan habitats. Sci. Agr. **30**: 209-234.

———. 1950b. Variations in the silk spinning and locomotor activities of the larvae of the spruce budworm at different rates of evaporation. Trans. Roy. Soc. Can. XLIV, Sec. **3**: 89-101.

Westveld, M. 1945. A suggested method for rating the vulnerability of spruce-fir stands to budworm attack. U.S. For. Serv., Northeast For. Expt. Stn., Proc. Publ. 4 p.

SOME EFFECTS OF AIR POLLUTION ON *LUPINUS* IN THE LOS ANGELES AREA

David B. Dunn[1]
Botany Department, University of Missouri, Columbia, Missouri

The experiments discussed in this paper were not designed as a study of smog (air pollution) effects, but the data which accumulated seemed to shed some light on the matter of smog effects on plants. The cause of the accumulation of smog, in the Los Angeles area, and lists of plants affected have been published (Haagen-Smit 1952, Hull and Went 1952, and others) and will not be discussed here.

While working on the taxonomy of the group *Micranthi*, of the genus *Lupinus* (Dunn 1955) from 1940 to 1942, at the University of California at Los Angeles, genetic and breeding experiments were conducted and there was no visible plant damage to colonies of the same seed stock as the plants discussed below. Again after World War II, the problem of the breeding systems of the group *Micranthi*, of *Lupinus* (Dunn 1956) was studied at the University of California at Los Angeles, during 1946 and 1947, and again there was no visible plant damage. In the spring of 1948 colonies of the parental stock and F_1 and F_2 populations of a number of genetic crosses were grown on the California State Polytechnic College campus, at San Dimas, California, without any apparent plant damage. In the fall of 1949 a screenhouse was built in Highland Park (Los Angeles) at my home on Avenue 50 near Monta Vista for planting lupines under conditions approximating those in nature (termed control for the plants grown at the Earhart Laboratories). Plantings were made at both places on December 15, 1949. The plantings at the Earhart Laboratories were made in washed, sterilized sand, in sets of ten seeds for each plastic container, for each variation of the environment, as shown in Table I. With 11 sets of conditions and 8 colonies of plants tested, a total of 880 seeds was used. With the method of hand chipping the seed coat of each seed, only three seeds failed to germinate and grow. The control plants in the screenhouse, in Highland Park, had no temperature or light regulation, while the plantings at the Earhart Laboratories (Went 1950b, 1957) were maintained at 20°C day temperature and 14°C night temperature, without light modification until January 21, 1950. At that time, the ten carts, each with trays of the eight colonies, were given the variations of temperature and daylength shown in Table I. At this time the plants in the Earhart Laboratories had 8-10 leaves each, while the control plants in the open screenhouse had only 3-5 leaves each, as a result of colder night temperatures.

The Earhart Laboratories are closed chambers, all materials being sterilized before entering and the workers changing their clothes before entering. The air circulating in the controlled chambers, at the time of this experiment, had passed through an electrostatic precipitator, which removed particulate material of particle sizes ranging from 2-20μ, after which the air passed through a water spray, for the purpose of cooling (Went 1950b). Dr. Went has been able to maintain the control chambers free from fungus infections and virus infections, since both spores and insects are removed from the entering air current. Spore counts have been reported as very low by Dr. Went and none of the workers have had any trouble with plant infections (Went 1950b). While this was beneficial from the standpoint of elimination of fungus infections, it was partially detrimental in the case of *Lupinus*, since these plants are legumes, which depend, normally, on root nodules for their supply of nitrogen, and none developed on the plants in the laboratories. The lupines grown in the Earhart Laboratories did show nitrogen deficiency, and were weaker than the control plants.

Of the colonies shown in Table I, all but No. 2157 had uniform seed patterns indicative of a high degree of homozygosity, as also suggested by the breeding experiments conducted by the author, which had shown these taxa to be virtually obligatorily selfed. Colony No. 2157 displayed a variable seed coat pattern in nature, suggesting some percentage of natural crossing. This is the colony postulated (Dunn 1955) as being as close to the ancestral type as it has been possible to locate. It is notable then that this colony, which had displayed heterozygosity in seed patterns, should also demonstrate the greatest adaptive range and hence the greatest flexibility. The oligate-selfed taxa with the high degree of homozygosity were relatively inflexible with narrow ranges of tolerance. Perhaps only in such taxa

---

[1] I am indebted to Dr. F. W. Went and Dr. George W. Beadle for the privilege of raising the colonies of *Lupinus* in the Earhart Laboratories, in 1950.

TABLE I. The number of plants that survived under each of the different growth conditions in the Earhart Laboratories in 1950 is shown. Ten plants were started and two were collected from each colony in each environment, so the number shown is the number that survived out of the remaining eight

Hours light	Night temperatures	L. bicolor subsp. microphyllus 1414**	L. bicolor subsp. umbellatus Wms. 42	L. bicolor subsp. umbellatus 2157	L. bicolor subsp. umbellatus v. trifidus 2596	L. bicolor subsp. marginatus 2245	L. bicolor subsp. tridentatus 2121	L. bicolor subsp. tridentatus v. rostratus 2211	L. bicolor subsp. piper-smithii 2205c
12	17°C	2 left	all died	3	all died	1	all died	1	1
8	17°C	1	all died	3	all died	all died	1	1	all died
12	14°C	6	all died	7	all died	2	1	all died	2
8	14°C	1	all died*	3	all died	2	all died	all died	1
12	10°C	all died*	1	6	2	3	all died	all died	1
8	10°C	3	all died*	5	1	2	2	all died*	1
12	6°C	6	5	5	1	1	all died	1	1
8	6°C	6	3	7	1	1	all died	1	1
12	3°C	3	5	1	all died	all died	all died	all died*	1
8	3°C	3	3	3	3	1	1	1	2
Control		Flr. blk.	Flr. blk.	Flr. blk.	Flr. blk.	killed	killed	killed	killed

* In flower, at the time the last plant died.

** The numbers for the colonies are field collection numbers cited in Dunn (1955) and have herbarium vouchers some of which are widely distributed and others will be distributed or are available upon request of material.

would it have been possible to obtain data on the lethal effects of smog on some plants. However, that does not in any way nullify the experiment, nor the conclusion that there are serious physiological effects from smog.

Colony No. 1414, which showed the next best adaptive range, was from seed originally collected in a vacant lot in Los Angeles and may be interpreted as having gradually, through selection, acquired some degree of resistance to smog. The colony "Wms. 42," was from Santa Rosa Island and the colony No. 2596 was from near Monterey, California. These four colonies represent one phylogenetic, evolutionary branch within the species *Lupinus* bicolor. They were from near the coast and in the control colonies, grown in the screenhouse, all of these colonies survived the "smog" with only vegetative damage and blockage of the floral development, except during periods of relatively clear weather, when they set flowers and fruit. In contrast the remaining four colonies were killed completely in the control plantings in the screenhouse. These latter four colonies represent subspecific taxa within the other phylogenetic branch within the same species *Lupinus bicolor,* and have developed in inland valleys and mountain areas in a hotter climate than those of the coastal region.

The effects of smog on the colony "Wms. 42" are shown in Table II, as an example of one of the colonies in which none of the plants died from smog in the control planting in the screenhouse but in which there was vegetative damage and blockage of floral development. By blockage of floral development I am referring to a condition in which the floral bracts were present and developed to normal size but the flower bud was killed at a very early stage and remained as a dead bud in the axil of the bract. The data for the plants within the Earhart Laboratories were collected each Saturday so the number of plants which had died during the week is shown. In each case the leaf burns and the development of a chlorotic condition were noted from 1 to 2 weeks prior to the time of death of the plants and complete records were kept. During the growing period, pressed herbarium samples were made twice and those that matured were sampled a third time. Hence, there was a chance for 8 plants to mature under each set of conditions. The use of a bracket after a number indicated that the last member of the colony was killed. While none of the plants of the colony "Wms. 42" was killed by smog in the screenhouse, the combined effects of smog and nitrogen deficiency rendered them susceptible in the Earhart Laboratories. There appears to be a greater susceptibility at the higher night temperatures and to a lesser degree, more susceptibility with an increased period of light. All were maintained at a 20°C day temperature throughout the entire experiment. This would suggest that metabolic processes are concerned with smog damage and not a photochemical reaction within the plant. Secondly, there was no blockage of the floral development in any of the colonies within the Earhart Laboratories suggesting that the smog damage in *Lupinus* was due to at least two different compounds, one of which was apparently water soluble, at least to the extent that a sufficient amount of the gaseous compound was removed by

TABLE II. The timing of the loss of plants of the colonies of *Lupinus bicolor* subsp. *umbellatus* (Wms. 42) under different growth conditions in the Earhart Laboratories in 1950, caused by air pollution (Smog)

Hours light	Night temperatures	December 1949			January 1950				February				March				April 1950			
		15	22	30	7	14	21	28	4	11	18	25	4	11	18	25	1	8	15	22
12..........	17°C										1			5	1	1)				
8..........	17°C												1	1	3		2)			
12..........	14°C									1				1	3	2)				
8..........	14°C												1	1		3	2)			
12..........	10°C														1		4	2		
8..........	10°C														1		1	5)		
12..........	6°C										1						1	1		
8..........	6°C																4	1		
12..........	3°C															1		1		
8..........	3°C																1		4	
Control.....													*				*			
Total losses**										1	2	0	2	8	9	7	15	10	4	

* Severe vegetative damage but no deaths.
** Total losses refers to the sum of the losses which occurred within the laboratories during each weekly period.

the air washing process so that the plants in the Earhart Laboratories were all able to flower, if they were able to survive that long. Solid particles could not enter the plant surface and be involved in the physiology without being dissolved. The killing compound in smog, however, had penetrated the air washing procedure and hence was neither a solid particle nor was it readily water soluble, suggesting therefore that it was probably a hydrocarbon. Concurrent with the vegetative damage which occurred in the colonies of *Lupinus,* other plants of sugar beets, *Achillea* and *Mimulus,* which were being grown in the Earhart Laboratories, were also seriously injured vegetatively by smog. The blockage of floral development is not known, at present to my knowledge, in plants other than *Lupinus.*

The effects of smog on the experimental colonies of No. 2211 are shown in Table III, as an example of those colonies which were killed completely in the outdoor screenhouse. This colony was much more sensitive than the colony "Wms. 42." Only 5 plants were lost in the latter before March 11th, while most of the plants under all conditions in colonies of No. 2211 had been lost by this date. Most of the plants which survived the first siege of smog were lost when the second siege set in during the week before April 1. Only 5 individual plants of No. 2211, apparently more resistant, survived and set seed in the Earhart Laboratories, while none were able to produce flowers in the screenhouse. The same situation prevailed with colony No. 2121. The sensitive plants were lost first at the higher night temperatures, while any effects of daylength were not apparent. Since plants were lost a full month earlier, at 10°C and 17°C night temperatures in the Earhart Laboratories, than those lost in the screenhouse, it may be suggested that the relatively lower night temperatures both in the Earhart Laboratories and in the screenhouse apparently offered some temporary protection from the smog effects. The fact that some plants did mature inside the Earhart Laboratories in colonies of No. 2211 suggests that some part of the killing material in smog was at least partially removed in the washing process. The air inside the controlled Earhart Laboratories had still been irritating to the eyes after the water washing prior to the installation of the charcoal filters. However the problem was not solved until Dr. F. Went and his co-workers had found that activated charcoal would adequately remove the toxic components from the air and had installed activated charcoal filters.

None of the plants were lost among the subspecies of *Lupinus* bicolor, until they had from 15 to 24 leaves, suggesting that in addition to temperature as a factor, there is apparently a physiological period or degree of development which must be reached before the plants become sensitive to smog. It will be noted that the plants were maintained at a 14°C night and a 20°C day temperature until January 21 at which time the plants in the Earhart Laboratories had from 7 to 10 leaves and not a single plant was lost to smog, which was present before Feb. 4th. Subsequently colonies of both No. 2211 and "Wms. 42" were lost entirely, at both the 8 hour and 12 hour day length and 14°C night temperature, with the same 20°C day temperature as before. These observations on temperature relationship are in accord with studies made by Geiger (1950), Hull and Went (1952), and Went (1957 & 1950a).

In the screenhouse in Highland Park several other species of lupines were raised with various responses to the smog. *Lupinus carnosulus* and

TABLE III. The timing of the loss of plants of the colonies of *Lupinus bicolor* subsp. *tridentatus* var. *rostratus* (No. 2211) under different growth condtions in the Earhart Laboratories in 1950, caused by air pollution

Hours light	Night temper-atures	December 1949			January 1950				February				March				April 1950			
		15	22	30	7	14	21	28	4	11	18	25	4	11	18	25	1	8	15	22
12..........	17°C								2	1	4									
8..........	17°C									2	2	1	1	1				1		
12..........	14°C										2		1	1			3)			
8..........	14°C										1	2	2	2)						
12..........	10°C										1		2	1			2		1)	
8..........	10°C								2		2	1	4)							
12..........	6°C												1	4	1					
8..........	6°C										1		2	1			2	1		
12..........	3°C								1	1			2	2	1					
8..........	3°C												3				1	1		
Control.....													6				2)			
Total losses*.									5	4	13	4	18	12	2	0	8	3	1	

* Total losses refers to the sum of the losses which occurred within the laboratories during each weekly period.

Lupinus sparsiflorus and *Lupinus confertus* appeared to be normal, healthy plants until they reached a stage of growth with 10 to 12 leaves and then all were killed in a few days time. *Lupinus arizonicus* developed very large vigorous plants with no apparent vegetative damage whatever, but the flowers failed to develop in the axils of the bracts, just as in the *Lupinus* bicolor complex. During a period of clear weather, that lasted about two weeks, several verticils of flowers developed, and set seed subsequently, but later several verticils were again blocked, after the smog accumulated.

In an outdoor field planting of a simulated population of *Lupinus nanus* 150 plants were started and all were destroyed by the 10-12 leaf stage of development. A second planting was also destroyed and only 8 plants of the third planting survived until clearing winds permitted flowering and fruit development. *Lupinus nanus* requires insect aid in pollination and has a fair amount of heterozygosity but that did not insure survival. The only species raised which showed no effects to either vegetative parts or flowers was *Lupinus micranthus,* a species obligatorily selfed.

Among the genetic studies attempted, an F_2 population of a cross (between subsp. of *L. bicolor*) between a relatively resistant taxon and a relatively sensitive taxon happened to be planted. One planting was on the bench on the south side in the screenhouse and part of this population was sensitive and was killed. The reciprocal cross, also an F_2 population, happened to be planted on the bench on the north side in less intense light and hence generally a lower temperature. In this population none of the plants died from the smog but quite a number were unable to set flowers until late in the season after a period of clearing winds. This corresponds to the temperature relationship observed in the Earhart Laboratories. It should be noted that all plantings in the screenhouse were on a three inch center to center plan, so that had there been any fungus attack, such as damping off, a whole plot of plants would have been destroyed. No such losses occurred.

During 1955, breeding experiments were conducted on some annual and perennial lupines at the Rancho Santa Ana Botanic Garden, at Claremont, California. *Lupinus latifolius,* an herbaceous perennial, up to six feet tall, had the floral mechanism blocked as described above, without any apparent vegetative damage. The shrubby species, *Lupinus arboreus, L. longifolius, L. excubitus,* and *L. albifrons,* all appeared to be resistant to smog and showed no floral damage, although this resistance may prove to be due to leaflet abscission of the leaflets affected. The annual, *L. densiflorus* and its allies appeared to be quite sensitive, with the entire plants dying within a week after one severe, three day siege of smog. The nature and manifestation of smog injury has been described by several authors (Middleton *et. al,* 1950; Bobrov 1952, Korietz & Went 1953, and Haagen-Smit, *et. al* 1952).

The types of damage observed in *Lupinus* (see Fig. 1) which have been considered as being due to smog, may be grouped in the following five catagories: 1) Mild damage, a curling of the leaflets, with no apparent dead patches; it would go unnoticed by someone not working with the group of plants for a long period of time. 2) The destruction of patches of leaf tissue; certain ages of leaflets were more sensitive, 3) A successive destruction of the leaflets until the plants were so weakened that they died. 4) No apparent vegetative damage, but complete blocking of the floral development, during periods of smog. 5) Both vegetative damage and the blocking of floral development.

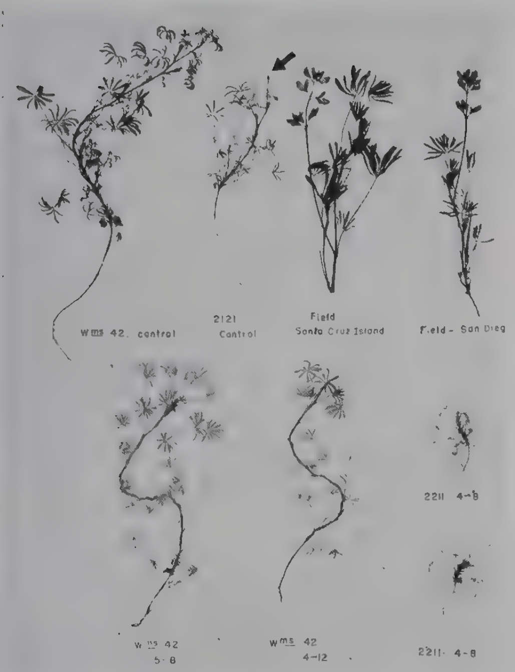


FIG. 1. Types of damage to *Lupinus* from air pollution. Two field specimens are shown in the upper right, both are *L. bicolor* subsp. *umbellatus*. The two control specimens, upper left were in the screenhouse and show the curling of the leaflets, while 2121 (*L. bicolor* subsp. *tridentatus*) shows a raceme which failed to produce flower buds. Both specimens of Wms. 42, lower left, were grown in the Earhart Laboratories at the temperature and day length indicated and both had three-fourths of the leaves dead from the combination of nitrogen deficiency and "smog," the upper leaves were nearly dead with only a few green patches left. The two specimens at lower right were completely killed and have only the yellow dried leaves left (2211, *L. bicolor* subsp. *tridentatus* var. *rostratus*).

In summary, it may be stated that there is evidence of susceptibility and resistance to smog, within the subspecific taxa of a single species, suggesting that the heredity of the plants is involved, giving some a marked advantage in survival in the Los Angeles area. Secondly, the evidence suggests that there are at least two compounds present in smog, which have an effect on survival and reproduction in *Lupinus*. One compound is apparently water soluble to a fairly high degree while the other is apparently essentially insoluble in water. Thirdly, the toxic material is gaseous and not particulate. The substance, which is irritating to the human eye, was a substance which was essentially insoluble in water and may possibly have been the same substance which was toxic to the vegetative parts of various plants within the Earhart Laboratories in 1950, since both occurred within the laboratories. Fourthly, the fact that the correlation of sensitivity to smog was highest with the plants given the higher night temperatures, while all of the plants were maintained at the same day temperature, and there was only a slight correlation with the plants given longer photoperiods, suggests rather strongly that the effects of smog on plants are involved with the metabolic processes. Higher temperatures increase the rate of metabolism and those plants maintained at the higher night temperatures were the most sensitive. (See also Hull and Went, 1952 and Went 1950a, 1957.) Finally the fact that the local subspecies in Los Angeles was more resistant to smog and was able to produce flowers and seeds more readily than any of the other subspecies from other parts of California, while several were killed outright, suggests very strongly that smog has been a subtle, selective agent over a rather extended period of time. I therefore suggest that the various gaseous fumes of large cities may well be active as selective agents in the local plant population even though these fumes have not reached the concentration necessary to become annoying to the people of the city.

REFERENCES

Bobrov, R. A. 1952. The anatomical effects of air pollution on plants. Proc. of 2nd Nat. Air Pol. Sym. 129-134.

Dunn, D. B. 1955. Taxonomy of *Lupinus*, group *Micranthi* (*Leguminosae*) of the pacific coast. El Aliso. **3**: 135-171.

———. 1956. The breeding systems of *Lupinus*, group *Micranthi*. Amer. Mid. Nat. **55**: 443-472.

Geiger, R. 1950. The climate near the ground. Trans. from German. Avail. at Harv. Univ. Pres. 1950.

Haagen-Smit, A. J., Darley, E .F., Zaitlin, M., Hull, H. M., and W. Noble 1952. Investigation on the injury to plants from air pollution in the Los Angeles area. Pl. Physiol. **27**: 18-34.

Hull, H. M. and F. W. Went. 1952. Life processes of plants as affected by air pollution. Proc. of 2nd Nat. Air Pol. Sym. 122-128.

Korietz, H. G. and F. W. Went. 1953. The physiological action of smog on plants. I. Initial growth and transportation studies. Pl. Physiol. **28**: 50-62.

Middleton, J. T., Kendrick, J. B., Jr., and H. M. Schwalm, H. M. 1950. Smog in the south coastal area. Calif. Agric., Univ. of Calif. **4**(11): 7-10.

Went, F. W. 1950a. The general problem of air pollution and plants. Proc. First Nat. Air Pol. Sym. 148-149.

———. 1950b. The Earhart plant research laboratory. Chron. Bot. **12**: 89-108.

———. 1957. Experimental control of plant growth. Chron. Bot. **17**.

AN ECOLOGICAL INVESTIGATION OF TWO DESERT TOBACCOS[1]

Philip V. Wells
Department of Biological Sciences, University of California at Santa Barbara

Introduction

Two species of Nicotiana are widespread in the deserts of intermountain western North America. *Nicotiana attenuata* Torr. dominates the cold deserts of the Great Basin, while *N. trigonophylla* Dun. is restricted to warm deserts from southern California to Texas and southward into Mexico. These species are rather mesophytic herbs with relatively thin, broad leaves. Nevertheless, both species have a long growing season and often attain a substantial size (over 1 meter), despite the very low rainfall over a considerable portion of their ranges.

An ecological study of these two species was made in the summers of 1956 and 1957 over most of their range in the United States. A total of 71 populations was investigated, 40 for *N. attenuata* and 31 for *N. trigonophylla.* The approximate locations of stations visited are indicated on the map in Figure 1. At each station, observations were made on physiography, elevation and surrounding vegetation, and at 58 stations, a soil sample was taken from around the roots of the tobaccos for subsequent analysis. Specimens from most of these populations are deposited for reference in the Duke University Herbarium. Also, all insects encountered on the tobacco plants were collected, and notes were taken on pollinators.

The field studies were supplemented by physiological investigations conducted in the laboratory at Duke University, and by a survey of collection data at many of the larger herbaria in the United States.

Results

General distribution

Nicotiana attenuata, an annual, has been found from about 50° N. Lat. in British Columbia south to 29° N. Lat. in Mexico, and ranges from California and Guadalupe Island east to Montana, Wyoming, Colorado, New Mexico, and western Sonora. The species is by no means evenly distributed over this large range. It achieves importance in terms of frequency and abundance chiefly where Great Basin vegetation dominates, that is, from southern Oregon and Idaho southward east of the Sierra Nevada to Owens Valley, across Nevada and southeastward to New Mexico, mainly in the higher country north of the Mogollon Rim. The altitudinal range is from 400 to 10,000 feet. In the warm desert latitudes, especially in the Mojave Desert, this species is largely confined to moderately high altitudes (pinyon-juniper zone), occurring lower if the site is sufficiently moist.

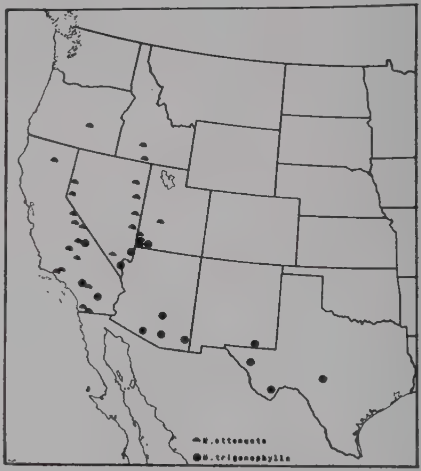


Fig. 1. Map showing location of *Nicotiana* stations investigated by the writer in the summer of 1956.

Nicotiana trigonophylla, a facultative perennial, ranges at about 37° N. Lat. from California east of the Sierra Nevada eastward to southwestern Utah and southward through all the warm deserts from California to Texas to about 16° N. Lat. in Oaxaca, Mexico. The recorded altitudinal range is from sea level to 9,500 feet, but in the northern part of the range it occurs mostly below 5,000 feet.

It is known that *N. attenuata* was extensively used by western American Indians as a narcotic, and even cultivated by them in desultory fashion. Hence, it is difficult to say how much of the present range of this species is due to the Indians. Also, *N. attenuata* has unquestionably increased in abundance and probably in range since the advent of the white man's road systems, since the roadside is currently by far the most common habitat for this tobacco.

Distribution in relation to climate

For these large ranges, only certain generalizations about the climate can be made. The western Great Basin, and the Mojave and western

---

[1] Doctoral Dissertation, Duke University, 1958. The author wishes to acknowledge the financial support of the research through a Duke University Tobacco Research Fellowship and certain travel expenses from National Science Foundation Grant 3834.

Sonoran Desert (Colorado Desert) lie in the rain shadow of the California cordillera and are characterized by scanty winter precipitation and summer drought.

Eastward, toward the Rocky Mountains, summer advection of unstable air masses from the Gulf of Mexico contributes an increasingly important fraction of the yearly precipitation, in the form of thunderstorms; here, precipitation in summer may equal or exceed the winter precipitation.

Most of the *N. attenuata* range is characterized by a considerably higher mean winter precipitation and a lower year-round mean monthly temperature than that of *N. trigonophylla*. This means a more favorable water balance for *N. attenuata*: a given soil moisture capital will be expended less rapidly because of reduced potential evapotranspiration.

Distribution in relation to physiography

Observations on this factor were made for all stations. In addition, habitat data were taken from herbarium collections at the following institutions: Bureau of Plant Industry, Missouri Botanical Garden, New York Botanical Garden, Rancho Santa Ana Botanical Garden, University of California at Berkeley, U. S. National Herbarium. Of the 606 specimens examined, only 193, or less than one-third, had any habitat information on the label. There were 76 records of *Nicotiana trigonophylla* and 6 of *N. attenuata* from bedrock outcrops and talus sites; 73 and 28, respectively, from beds of intermittent watercourses; and 12 and 94 from roadsides, trailsides, earthmounds and ditches. Of the ruderal categories, the roadside is most predominant, accounting for all 12 *N. trigonopylla,* and for 63 of the *N. attenuata* ruderal collections. A category which may be classed as ruderal (but hardly physiographic) is the vegetation burn, for which an additional 8 instances were noted for *N. attenuata.*

The various habitat types are all subject to periodic disturbance. Also, they are probably all favored in regard to the water factor. In support of the latter statement, consideration will be given individually to the different types of habitats.

Rock outcrops.—*N. trigonophylla* is usually found either in a rock crevice on a cliff, or at the base of a cliff or talus boulder. The surrounding expanses of bare rock make excellent watersheds, while the nooks and crevices inhabited by the tobacco serve for catchment of the run-off. It is easy to see that the effectiveness of rainfall could be greatly multiplied by this concentration.

Roadsides.—Here there is a combination of the large, impermeable road surface, acting as a watershed, with the more porous gravelly shoulder acting to catch the runoff. Naturally, a surfaced road will be a more effective watershed than a dirt or gravel road, but the latter are most often so impacted by traffic as to allow very little infiltration. In like manner, even cattle trails and ordinary footpaths may serve as watersheds, benefiting the trailsides. In the Great Basin deserts, it is a common observation that the growth of big sagebush (*Artemisia tridentata*) is much more luxuriant along abandoned roads than on the surrounding plains (Billings 1949), and there are many other plants which illustrate the same principle.

Intermittent watercourses.—Periodically, the dry streambeds of desert and semi-arid country are flooded following the erratic rains, and are thus naturally surface irrigated. This is evidently the chief source of water for tobaccos growing in washes, since they are most often too shallowly rooted to act as phreatophytes like mesquite (Prosopis), which sends roots down to the water table. However, if the water table in a dry wash were situated close to the surface, but below the depth of tobacco root penetration, it is conceivable that a combination of capillary rise and subterranean dew formation might bridge the gap between plant and water. The dew principle is rendered feasible by the great daily temperature fluctuations in the superficial alluvial layers. At night, the surface layer will become cooler than the lower layers, which are moister by virtue of proximity to the subjacent water table. Since vapor pressure gradients determine the direction and rate of diffusion, the movement of water vapor would be from the warm, moist subsoil to the cool dry surface, where condensation, or direct absorption by roots and soil might take place (Lebedeff 1928).

Distribution in relation to soil

Soil samples were collected in the immediate vicinity of the roots of the tobaccos at 58 different stations, 36 for *N. attenuata* and 22 for *N. trigonophylla.* These samples were investigated with respect to texture, water retention capacity, salinity, and pH.

Parent material.—The common occurrence of *N. trigonophylla* directly on bedrock affords an opportunity to compare its frequency on different types of parent rock material. There were 15 collections from limestone, 9 from basalt, 8 from granite, 6 from (mostly lime-cemented) sandstone, and 3 from gypsum.

Eighty per cent of these occurrences were on calcareous rocks (basalt is high in calcic plagioclase and crevices in it are invariably lime-whitened). Furthermore, all *N. trigonophylla* soil samples gave a positive, often extremely vigorous, test for carbonate with HCl. By comparison, only 47 per cent of the *N. attenuata* soils showed any evolution of gas at all. That the carbonate was probably mostly lime, and not soda, is shown by the circum-neutral pH of all the *N. trigonophylla* soils (see below, under pH). From these data, *N. trigonophylla* might be classed as calciphilous, though not necessarily obligate in this respect. *N. attenuata* was seldom found on bedrock, and the fact that half of its soils showed a positive carbonate reaction may be mostly due to the common use of limestone gravel in roadbeds.

The absence of any collections of *N. trigonophylla* from mudrocks correlates with its widespread occurrence on coarse-textured soils (see below).

Texture.—The results of granulometric analysis by the hydrometer method of Bouyoucos (1936), given as mean per cent composition, were, for *N. trigonophylla* soils, gravel 35.2%, sand 48.9, silt 11.4, and clay 4.0. Soils supporting *N. attenuata* measured 28.0% gravel, 55.8% sand, 11.5% silt, and 4.7% clay.

Perhaps a more sensitive comparison of the soils of the two species is afforded by a frequency distribution plot of the same data, which shows modal concentrations (Figure 2); the 5 per cent composition class intervals were chosen arbitrarily. Sand and gravel are variable and there is a tendency towards substitutions of one for the other, while silt and clay are fairly constant, at a low level. In general, there is a remarkable resemblance in texture between the two series of soil samples collected.

The prevelant coarse texture suggests a high degree of infiltration, drainage, and aeration, but also low water retention and low ion-exchange capacity. A possible compensation for the latter deficiencies is the fact that the clay fraction in most of the soil samples appeared to be montmorillonitic, judging from the amount of swelling and puddling upon addition of water.

Water retention capacity.—Analyses were made of water content (as per cent of oven-dry weight) at several soil moisture tensions from 0 to 15 atmospheres, using the porous plate and pressure membrane apparatus (Richards 1947, 1948). The results are plotted as a frequency distribution with class intervals of 2.5 per cent (Figure 3).

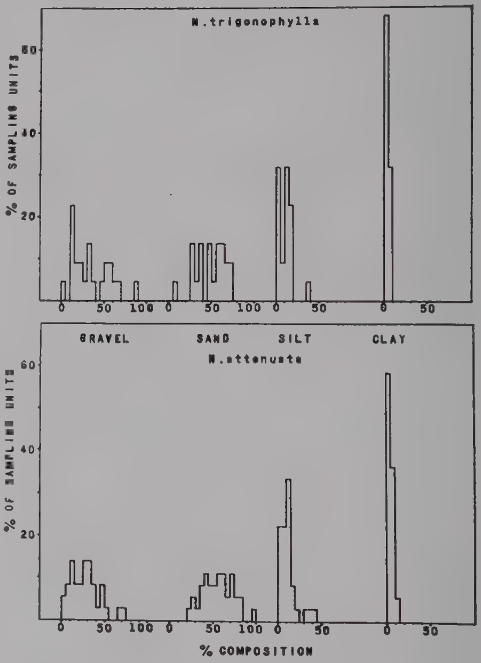


FIG. 2. Frequency distribution plot of mechanical analysis data, based on 58 soil samples: 36 for *N. attenuata* and 22 for *N. trigonophylla.*

Paralleling the similarity in texture, there is a strong resemblance between the two sets of soil samples in regard to water retention. However, at the 15 atmosphere level, the *N. attenuata* modal values are skewed towards somewhat higher water retention capacity than are those of *N. trigonophylla.*

Salinity.—Saturation extracts of the soils were prepared following the method of Richards (1954). Their electrical conductivity was determined with a conductivity cell and direct indicating bridge (Solu Bridge RD, Industrial Instruments Inc.), which was calibrated against a series of standard KCl solutions. The saturation values thus obtained were converted to field capacity values by multiplying by the ratio:

$$\frac{\text{saturation water content}}{\text{field capacity water content}}$$

Field capacity is a more realistic level than saturation, but it involves a reduction in volume of soil solution sufficient to bring about complications due to precipitation of salts, notably gypsum. The conductivity data were converted into osmotic pressures, expressed in atmospheres, by means of a nomograph in the work cited above (Richards, 1954). The results are shown in Figure 4 as a

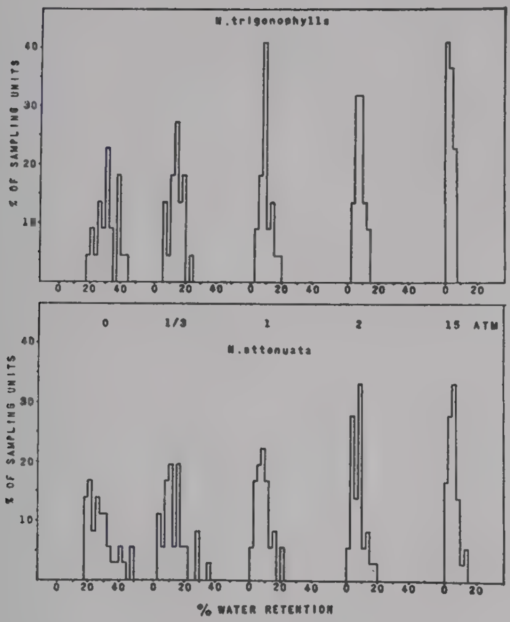


FIG. 3. Frequency distribution plot of water retention capacity data based on 36 soil samples for *N. attenuata* and 22 for *N. trigonophylla.*

frequency distribution plot, with 0.5 atmosphere class intervals. For both species, the soil solutions at most stations are below 1.0 atm. osmotic pressure at field capacity, and these soils may be termed non-saline. However, the mode for *N. attenuata* is skewed towards lower osmotic pressures than the mode for *N. trigonophylla,* which is skewed in the opposite direction. Also, *N. trigonophylla* occasionally occurred on soils ranging in salinity from 3 to 16 atm. at field capacity, but for *N. attenuata* only one population deviated much from the mode. At saturation, the maximum values for the two species would reduce to 7.1 and 1.8 atm., respectively, and it is possible that an overestimate has been made in calculating field capacity values without taking gypsum precipitation into account.

Hydrogen ion concentration.—The pH was determined on saturation extracts, using a Beckman meter. The results are plotted as a frequency distribution, with class intervals of 0.2 pH unit (Figure 4). The soils of both species have a strong mode in the circum-neutral range, but *N. trigonophylla* has such an especially restricted pH range as to suggest that buffering is involved. It is probable that there is a higher level of lime (calcium carbonate) and gypsum (calcium sulfate) in the warm desert soils on which *N. trigonophylla* occurs. Lime acts as a buffer against acidity, and the slightly soluble gypsum acts as a reservoir of calcium ion which may neutralize sodium carbonate alkalinity by combining with the carbonate radical to form highly insoluble lime, leaving neutral sodium sulfate in the soil solution.

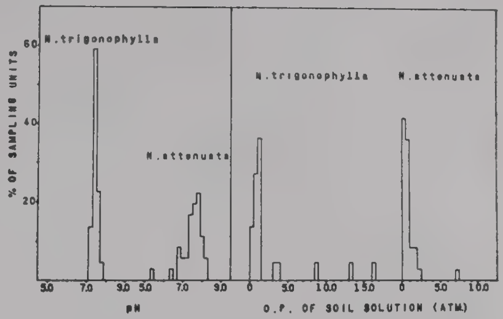


FIG. 4. On left: frequency distribution plot of pH data, based on 58 soil samples. On right: frequency distribution plot of salinity data, based on 58 soil samples.

Distribution in relation to vegetation

Over the wide geographic range of the two species, the associated vegetation varies not only floristically, but physiognomically. However, neither species is ordinarily immediately associated with undisturbed vegetation in the sense of forming a synusial or structural element within it. Rather, the occurrence is on disturbance sites of diverse origin, for instance, areas of alluvial or colluvial deposition such as dry washes and talus slopes, or such man-made niches as roadsides and ditches. Because of this tendency to occur in pioneer habitats, one might question the wisdom of investigating the surrounding climax vegetation, which is by definition excluded from the very sites on which the tobaccos grow. Nevertheless, there is indicator significance in perennial vegetation with respect to year-round climate, and this justifies at least a brief account of the frequency of occurrence (enclave-wise) of the two species in the major vegetation types. It must be kept in mind, however, that both species are able to germinate and produce seed during one favorable growing season, and are thus not necessarily limited in their ranges by adverse climate at other times of the year, as woody vegetation may be.

Associated Vegetation.[2]—Table I gives frequency of occurrence in various types of vegetation, based on 64 collections of *N. attenuata* and 42 of *N. trigonophylla.* It is evident that *N. attenuata* is common in a wider range of vegetation types than *N. trigonophylla,* which is largely restricted to the warm desert types. The modal occurrence-class for the former is northern, or cold desert shrub, and for the latter southern, or warm desert shrub.

---

[2] Nomenclature as in Kearney and Peebles (1951).

TABLE I. Distribution in relation to vegetation

Vegetation Type	Per Cent of Collections	
	N. attenuata	*N. trigonophylla*
Sierran coniferous forest (*Abies concolor, Pinus lambertiana, Libocedrus decurrens*, etc.)	2	0
Yellow-pine forest (*Pinus ponderosa*)	11	0
Deciduous oak forest (*Quercus gambelii*)	3	0
Evergreen chaparral (*Adenostoma fasciculatum, Quercus* spp., *Ceanothus* spp., *Arctostaphylos* spp., *Garrya flavescens* etc.)	9	0
Pygmy conifer woodland (*Juniperus osteosperma, J. monosperma, Pinus monophylla, P. edulis*, etc.)	25	10
Great Basin desert shrub (*Artemisia tridentata, Atriplex confertifolia, A. canescens, Chrysothamnus* spp., etc.)	41	5
Blackbrush (*Coleogyne ramosissima*)	3	24
Creosote bush-bur sage (*Larrea divaricata, Franseria dumosa*, etc.)	6	52
Giant cactus-paloverde (*Cereus giganteus, Cercidium microphyllum*, etc.)	0	10

Microsite associates.—Although both species appeared to be intolerant of competition by their almost universal occurrence on thinly vegetated or bare sites, one or more plant species of similar ecological character were invariably present. Table II lists all species found on the tobacco microsites at two or more stations; woody plants are indicated by an asterisk. It is, in part, almost a checklist of the more common pioneer or weedy species of lower altitudes in the Intermountain West.

TABLE II. Microsite associates

Associated with *N. trigonophylla*	Presence: Number of Stations	Associated with *N. attenuata*	Presence: Number of Stations
Tridens pulchellus	6	*Argemone platyceras*	12
*Prosopis juliflora**	5	*Salsola kali*	9
*Acacia greygii**	4	*Artemisia tridentata**	7
*Hymenoclea salsola**	4	*Bromus tectorum*	5
Bromus rubens	3	*Erodium cicutarium*	3
*Chilopsis linearis**	3	*Halogeton glomeratus*	2
Datura meteloides	3	*Cleome serrulata*	2
*Viguiera stenoloba**	3	*Mentzelia laevicaulis*	2
*Fallugia paradoxa**	2	*Pentstemon palmeri*	2
*Nicotiana glauca**	2	*Nicotiana trigonophylla*	2
N. attenuata	2	*Datura meteloides*	2
*Baccharis glutinosa**	2	*Chrysothamnus nauseosus**	2
*Parthenium incanum**	2	*Chrysothamnus pulchellus**	2

* Shrubs.

Factors controlling seed germination

Seed germination and seedling establishment are at once critical phases in the life cycle and amenable to experimentation. Hence, these phases were investigated in relation to a number of physiological factors, *viz.*, water availability, temperature, aeration, and light requirements. Seed collected in the field in small paper envelopes was stored in corked glass vials at room temperature.

Water availability.—Total soil moisture stress at any given soil water content is equal to the sum of soil moisture tension and osmotic pressure of the soil solution. For the purpose of measuring the effect of soil moisture stress on seed germination and growth of seedlings in the tobaccos, a graded series of mannitol solutions was used which would cover the range down to zero germination. These were: 2.4, 4.7, 7.1, 9.4, and 11.8 atm. About 175 seeds from each of four widely separated populations of each species were used at each osmotic level. The seeds were placed on filter paper in tightly capped jars containing the mannitol solutions, at a temperature of about 70° F. Germination was measured by a total count, and length of hypocotyl by measurement of about 40 seedlings at each level (necessarily less at low germination levels).

The results are plotted as mean percentage of the zero atmosphere control (distilled water) in Figure 5. Both species were strongly inhibited in germination and subsequent growth at osmotic concentrations of 11.8 atm. and above, but at 7.1 atm. *N. trigonophylla* was much less affected than *N. attenuata*. In fact, the percentage germination of the former was fourfold greater than the latter at this level.

These data indicate that *N. trigonophylla* should be more successful than *N. attenuata* in becoming established on soils with a salinity range of 4.7 to 9.4 atm. That this may be the case in nature is indicated by the soil salinity data for the two species. The highest salinity value found for the soils of *N. trigonophylla* at saturation was 7.1 atm. The calculated equivalent at the field capacity level was 16.1 atm. Corresponding figures for *N. attenuata* were 1.8 and 8.0 atm.

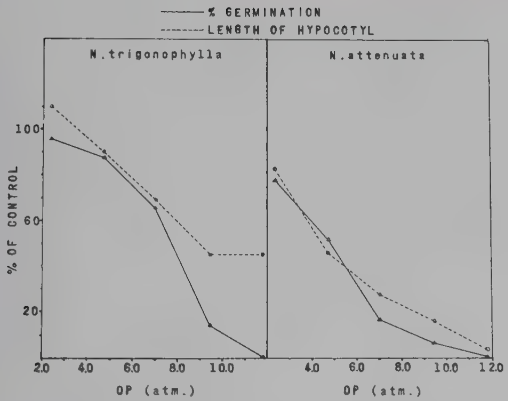


FIG. 5. The relation of germination and growth of seedlings of *N. trigonophylla* and *N. attenuata* to osmotic pressure.

The soil salinity data presented in Figure 4 represent field capacity values. While field capacity may be a more appropriate soil moisture level for salinity appraisal than saturation, it is probable that germination and establishment of the tobaccos take place on the more saline soils only when these are close to the saturation moisture content.

Temperature requirement.—Seeds of most populations of both species were placed on wet filter paper in petri dishes and exposed to available controlled temperatures to find the effect on germination. Seed from all *N. trigonophylla* populations germinated well over the range from 65° to 95° F., about three days after being wetted. No population of *N. attenuata* would germinate at these temperatures unless previously stratified at temperatures from 33° to 40° F.

Neither species would germinate if kept constantly in a refrigerator (intermittently lighted) at 33°-40° F., nor if placed in an oven at 107°-113° F. for only 3 hours a day, alhough kept at 70° F. for the remaining 21 hours.

Seed from different *N. attenuata* populations varied greatly as to stratification requirement. Most required 10 days or more for maximum germination, but one population from Leeds, Utah, gave 91 per cent germination following only three days of stratification at 33° to 40° F. The important point is that all *N. attenuata* seed requires some stratification (below 40° F.) before germination will take place. Since such stratification is not likely to occur in summer throughout most of its range, this constitutes an effective mechanism for preventing germination of seed in the summer, when establishment would be precarious because of the rapidity with which the soil surface becomes dry following rains. This stratification requirement may also play a part in determining the southern limit of range for *N. attenuata,* for if the climate lacked a sufficiently cold season, the *N. attenuata* seed could not germinate. On the other hand, mature *N. trigonophylla* seed can germinate within three days whenever the soil temperature is warm enough provided, of course, that water is available.

Since it is possible that both species might germinate during a season when killing frosts prevail at night, the effect of freezing the seedlings of both species was investigated. Numerous seedlings from populations representative of different parts of the range were frozen completely and allowed to thaw in the refrigerator; in every case, death of the seedlings resulted.

Facilities were not available to control temperatures below freezing, but seedlings representing 8 populations of *N. trigonophylla* (mostly from the northern part of its range) and 12 of *N. attenuata* (widespread) were grown in pots outdoors during late January and the first part of February, 1958. Temperature was measured next to the seedlings with a maximum-minimum thermometer. At this time, the Durham, North Carolina temperatures were ranging from 40° to 60° F. during the day, and down to 26° F. at night; the seedlings of both species appeared to do well under this regime. The night of February 10, the temperature dropped to 18° F. and by noon the next day, all 8 populations of *N. trigonophylla* had frozen and wilted beyond recovery, after thawing. On the other hand, none of the *N. attenuata* populations appeared to be much affected, and these continued to survive temperatures in the low twenties every night until February 17, when a new low of 10° F. was reached. This froze all 12 populations of *N. attenuata* and these wilted rapidly and died upon thawing.

Apparently, only fairly complete freezing is deleterious to these species in the seedling stage, and it appears that lower temperatures are tolerated by *N. attenuata* than by *N. trigonophylla.* In general, the geographic range of *N. trigonophylla* has about twice as many frost-free weeks as that of *N. attenuata.* The greater tenderness of *N. trigonophylla* seedlings to frost is probably a factor determining the northern limits of its range, since its non-dormant seed are apt to germinate in the fall.

Aeration requirement.—It was observed that *N. trigonophylla* would germinate under water. This led to the following experiment: 770 seeds of *N. trigonophylla* and 900 previously stratified seeds of

N. attenuata were placed at the bottom of separate 250 ml. Ehrlenmeyer flasks filled with distilled water. The flasks were tightly stoppered and set aside for two weeks in a lighted place. The *N. trigonophylla* seed germinated to the extent of 80 per cent of the control (seed germinated on moist filter paper in a petri dish), but the germination did not progress beyond emergence of the radicle. The *N. attenuata* seed showed no germination whatsoever.

However, when the stoppers were removed and air was bubbled through the water, the *N. attenuata* seed did germinate to the extent of 45 per cent of the control, but the germination progressed only as far as emergence of the radicle. The *N. trigonophylla* seed which had progressed to this stage in the stoppered flask, now proceeded with elongation of the hypocotyl and expansion of the cotyledons to the extent of 23 per cent of the control.

Another experiment was arranged where seeds of six populations of each species (using about 400 seeds per population, with the *N. attenuata* seed previously stratified) were placed at the bottom of 9.5 inches of stagnant distilled water in graduate cylinders. After two weeks, germination and seedling development were found to be as follows (Table III).

TABLE III. Variation in capacity for submerged germination

Tobacco population	Germination as per cent of control	Completion of seedling development as per cent of control
N. trigonophylla		
Texas	68	52
New Mexico	64	5
Utah	50	5
Arizona	49	5
Utah	37	4
Nevada	37	0
N. attenuata		
Utah	64	0
California	57	0
Utah	27	0
Nevada	18	0
California	12	0
California	0	0

Evidently, considerable variation exists among different populations of the same species with regard to submerged germination, but a distinct difference exists between the two species with respect to development of the seedling under these conditions. The development is inhibited at an early stage in all *N. attenuata* populations, but most *N. trigonophylla* populations tested have a small percentage of more complete development under water, and in the Texas population this amounted to over 50 per cent of the control.[3]

The ability to germinate under small depths of water may have survival value in the dry wash habitat. In the wake of the sporadic floods which rush down these watercourses, numerous shallow pools of water are left in low places; these persist for varying periods, but usually evaporate completely, in time. If seed should germinate at the bottom of one of these pools, there would be no danger of desiccation during the early growth of the seedling, and when the surface water eventually evaporated, the saturated soil would insure a soil moisture reserve for the maturing plant, lasting well into the dry season. Also, if germination took place during a season when nocturnal killing frosts were prevalent at the soil-air interface, seedlings germinating under water might be protected from freezing injury.

Since it is probable that *N. trigonophylla* may often germinate in this environment (numerous small plants were occasionally seen growing in the mud-cracked depressions of recently evaporated pools in arroyos), this constitutes an unusual case where a plant begins life as a "hydrophyte," matures as a "mesophyte," and may persist for some time after the onset of drought as a "xerophyte."

Light requirement.—Seeds from all populations of both species were found to require at least a short exposure to light before they would germinate. There was considerable variation as to the amount of light required among different populations. A five minute exposure to red light produced from 0 to 77 per cent of the germination of the continuous light control in *N. trigonophylla* and from 0 to 100 per cent in *N. attenuata.*

Red was the most effective part of the spectrum in promoting germination when light of approximately equal intensity, but of different quality, was employed. These results agree with published findings on a variety of light sensitive seeds (Toole, *et al.* 1956).

If a deductive approach may be taken, the question is: What is the ecological significance of red sensitivity for seed germination? It is known that the amount of diffraction or scattering of light by small particles or openings varies inversely as the fourth power of the wave length. Therefore, it seems likely that fine soil particles, and especially the finer interstices between them, might act to scatter blue light more than red. This means that red light would penetrate the soil to a greater depth than blue light, and that below the soil layer where the first scattering takes place (the surface), the penetrating light will be impoverished in the blue end of the spectrum compared to the incident light.

---

[3] Because of the very small size of the plants in the early stages of germination, dissolved and photosynthetic oxygen probably meets their respiratory needs. Mature plants appear to have a high root-aeration requirement.

An investigation was made of the transmission spectrum of a medium-coarse quartz sand and of a silty clay, with the Beckman DU spectrophotometer. It was found that a 5 mm. thickness of wet silty clay gave zero light transmission at all wave lengths measured, even when using a blank which reduced the slit area, and hence the level of the blank signal relative to the sample signal. Therefore, it was necessary to use a dilute suspension ("soil solution") and the blank for this sample was 5 mm. of distilled water. The wet sand was more translucent than the silty clay, but it was necessary to use an arbitrary blank which reduced the slit area, since with the usual slit openings, the blank gave such a high signal relative to the sample signal that the latter registered zero transmission at all wavelengths. This blank was a series of holes in black tape arranged in linear fashion, so that all fell within the slit image.

The transmission spectra of these soils in the wavelength range from 400 to 800 mμ are presented in Figure 6; a comparison of the ratios of percentage transmission of longer to shorter wavelengths is provided in Table IV.

Table IV. Ratios of light transmission at different wavelengths for soil materials

Sample	Per Cent Transmission Ratios	
	655 mμ/450 mμ	735 mμ/655 mμ
sand, 10 mm.	6.0	1.6
sand, 5 mm.	2.5	1.2
clay suspension	1.9	1.1

It is evident that the relative energy transmission in the shorter wavelengths is smaller than in the longer wave lengths when light is passed through these materials. The greater loss in the blue end of the spectrum may be due to specific absorption and refraction effects in addition to diffraction.

The soil-air interface is a relatively harsh environment. As the center of radiation exchange, it undergoes the most rapid and extreme temperature changes, and with regard to the moisture factor, it is alternately bombarded by splattering rain drops and subjected to severe droughts. Therefore, any depth below the surface, however slight, will be an improvement from the standpoint of an environment for germination of seeds.

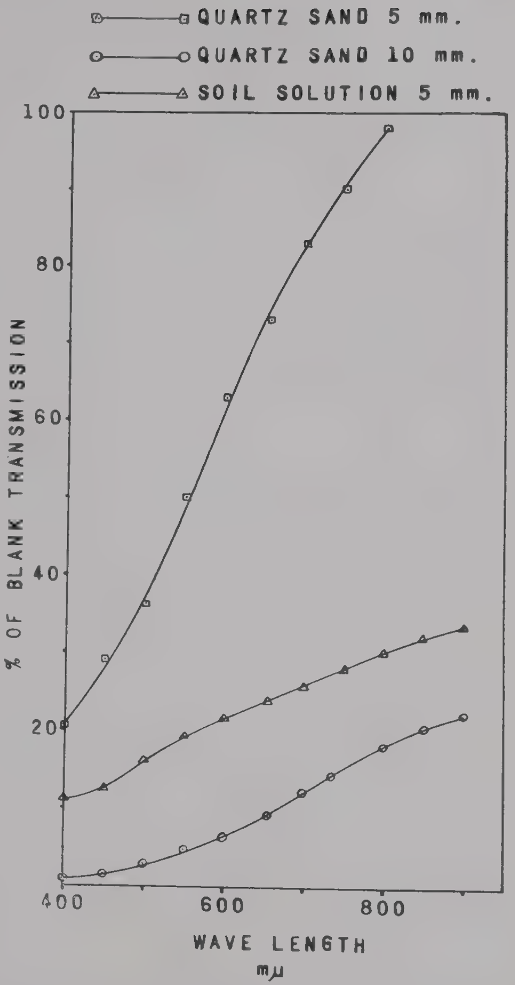


Fig. 6. Transmission spectra of soil materials.

If then, a seed is light-requiring, it is of some survival value for it to be red sensitive, since this property will facilitate germination at nearly the maximum depth of penetration of visible light. Of course, this will not prevent the seed from germinating on or near the surface, where the risk of early desiccation is greatest; it merely confers on the seed the capacity to germinate where this risk is diminished.

Radiation of 735 mμ wave length is reported to inhibit the germination of many light sensitive seeds (Toole, *et al.* 1956). Since 735 mμ light has a higher per cent transmission in soil than 655 mμ light (Table IV), it may be inferred that there is some level below the soil surface where the inhibiting effects of far red radiation will prevail. But since this level would be just above the zone of perpetual darkness, the only effect is to extend that zone upward, as far as light sensitive seeds are concerned.

These considerations suggest another question: What is the nature of light transmission by the seed coats? This was investigated for the two species of Nicotiana, both of which have dark brown seed coats. Twelve seeds were cut in half down the long axis, and the embryo and endosperm were scraped out of the seed coats under a dissecting microscope. The 24 seed coat halves were then tightly imbedded in a series of pinholes in black tape which were arranged to fall entirely within the slit image of the Beckman DU spectrophotometer. A single large pinhole in black tape served for a blank. The transmission spectrum of the seed coats over the wavelength range from 400 to 800 mμ is presented in Figure 7. The ratio of per cent transmission at 655 mμ to that at 450 mμ was 7.5 for the seed of both species, which gave nearly identical transmission curves.

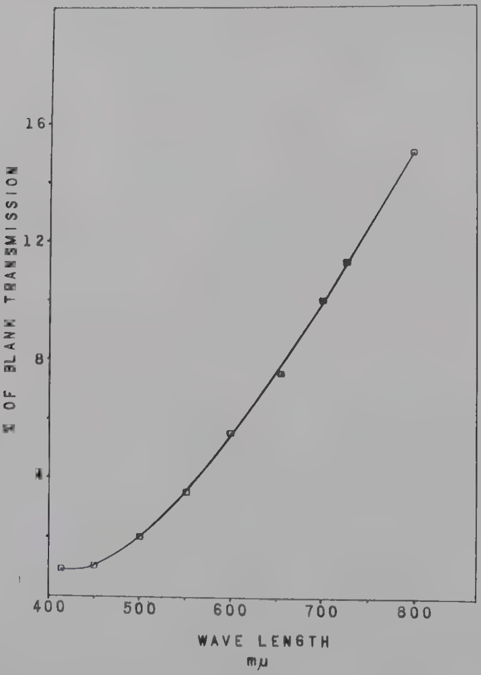


FIG. 7. Transmission spectrum of the seed coats of *N. trigonophylla.*

In order to establish the extent to which this difference in seed coat transmission accounts for the red light sensitivity in tobacco seed, it was necessary to have an accurate estimate of the amount of germination produced by known relative energies at the two wavelengths, 655 and 450 mμ. The small size of the Nicotiana seed made it possible to use the Beckman DU spectrophotometer itself as a light energy source for promotion of germination. The slit width was set at 0.5 mm. and the slit image was outlined on a strip of filter paper in a cuvette. The filter paper was then moistened, and seeds of *N. trigonophylla* (from Eddy Co., New Mexico) were carefully arranged in the rectangular slit image outline; an average of 100 seeds could be accommodated in this small space. More distilled water was added to the cuvettes, which were capped and placed in a light-tight box for 24 hours, to allow an adequate imbibition period for the seed. The cuvettes were irradiated in the spectrophotometer in a completely darkened room and replaced in the light-tight box for 5 days, during which time germination was completed. The results are presented in Table V. Dark controls gave zero germination. The mean ratio of per cent germination at 655 and 450 mμ was 7.3. With exposures longer than 5 minutes, the red light evoked only a slight additional germination response compared to the blue, which greatly reduced the response ratio of red to blue; in other words, the red light response reached a plateau while the blue light response was still climbing.

TABLE V. Effect of light quality on germination

Exposure Time (Minutes)	PER CENT GERMINATION		RATIO OF PER CENT GERMINATION
	655 mμ	450 mμ	655 mμ/450 mμ
5	82.6	10.3	8.0
4	70.7	9.6	7.4
2	61.1	9.9	6.2
2	60.1	7.8	7.7

A relative energy distribution curve for the tungsten lamp of the DU spectrophotometer was kindly supplied by Beckman Instruments, Inc. This indicates that the relative energy of 655 mμ radiation is about fourfold greater than 450 mμ radiation in this instrument (the wavelength of maximum energy in the emission spectrum of the tungsten filament at 3000° K may be computed from Wien's displacement law to be about 960 mμ). Since the relative energy transmission by the seed coat at 655 mμ is 7.5 times that at 450 mμ, the relative energy penetrating the seed coat at 655 mμ is 4 x 7.5 or 30-fold greater than at 450

TABLE VI. Temperature-light interaction in the germination of *N. attenuata* seed

No.	SEQUENCE OF TREATMENTS						RESULTS
	Dark Imbibition or Stratification			Dark Stratification	Dark Germination	Light Germination	Mean Per Cent Germination
	70°F	36°F	70°F	36°F	70°F	70°F	
1	24 hrs.	2 hrs. (*32°F)	—	5 days	7 days	—	73
2	24 hrs. (*70°F)	—	—	5 days	7 days	—	74
3	—	24 hrs.	2 hrs. (*70°F)	5 days	7 days	—	0
4	—	24 hrs.	—	5 days	7 days	—	2
5	—	5 days	2 hrs. (*70°F)	—	7 days	—	2
6	—	5 days (*32°F)	—	—	7 days	—	4
7	—	5 days	—	—	—	7 days	76
8	—	—	—	—	—	14 days	1
9	—	—	—	—	14 days	—	0

* 5 minute exposure to red light at the indicated temperature.

mμ, when the Beckman instrument is used as a light source.

However, the per cent germination induced at 655 mμ averaged only 7.3 fold greater than that induced at 450 mμ. If it may be assumed that the photochemical reaction involved in germination takes place inside of the seed coat, then the 7-fold greater germination response elicited by the 30-fold greater energy input at 655 mμ can hardly be interpreted as evidence for a photoreceptive pigment with an absorption maximum in the red. For these tobaccos, it would appear that the hypothetical photoreceptive pigment involved in light-induced germination may have a greater absorption in the blue end of the spectrum than in the red. The red maximum in the action spectrum may be due to a combination of greater transmission of red light by the seed coat, and greater output of energy at the red end of the spectrum by the light source.[4]

Temperature-light interaction.—Since *N. attenuata* seeds require both light and stratification before germination will occur, one might ask the question: What is the relative light sensitivity of these seeds before and after stratification? Table VI shows the results of an investigation along these lines, using seed collected from a population of *N. attenuata* near Leeds, Utah. The sequence is from left to right for each numbered combination of treatments, each of which was run in duplicate. The asterisks indicate the point at which the seeds were exposed to red light with an intensity of 7.6 foot candles for 5 minutes; the temperature during the light exposure is given next to the asterisk. It is apparent that the 5 day stratification period may either follow or precede the light treatment, but that a warm (70° F.) imbibition period on the order of 24 hours, prior to (or during) exposure to light, is necessary to produce a significant amount of germination. However, temperature has little effect on the photoreaction itself over the range from 32° to 70° F. Evidently, one or more dark reactions, which make the light reaction possible, proceed during imbibition at 70° F., but are inhibited at 36° F.

N. trigonophylla seeds need no stratification, but a comparison with *N. attenuata* in regard to the warm imbibition requirement was instructive. The sequence of treatments and results are presented in Table VII; the results are the means of duplicates. Light of 150 foot candle intensity was furnished during the warm imbibition phase, which, together with the preceding cold imbibition phase, made up a complement of 24 hours. The seed source for *N. attenuata* was the same as the above, and the *N. trigonophylla* seed was from Eddy Co., New Mexico. All *N. attenuata* seeds were given 5 days of dark stratification at 36° F. before the warm dark germination period.

It is noteworthy that *N. trigonophylla* seeds require less warm imbibition than *N. attenuata* before they become light sensitive. In nature, this could be a disadvantage: a 4 hour midday warm period during winter might elicit a 50 per cent germination of *N. trigonophylla* seed, but only about 8 per cent of *N. attenuata* seed would germinate, judging from the experimental results. This would leave fewer *N. trigonophylla* seeds in reserve in the event of killing frost. Since some

---

[4] The fact that the seed-coat transmission ratio of red to blue, and germination response ratio of red to blue were very close (7.5 and 7.3, respectively) suggests that the filtering effect of the seed coat could account for most of the apparent red light light sensitivity of these tobacco seeds.

TABLE VII. The effect of different warm imbition periods on seed germination

SEQUENCE OF TREATMENTS			RESULTS	
Cold Dark Imbibition	Warm Light Exposure	Dark Germination*	Germination Mean Per Cent of Control	
36°F	70°F	70°F	*N. trigonophylla*	*N. attenuata*
12 hours	12 hours	6 days	92	67
16 hours	8 hours	6 days	68	39
20 hours	4 hours	6 days	50	8

* For *N. attenuata* seed, this was preceded by a 5 day dark stratification at 36°F.

evidence has been presented above that *N. trigonophylla* seedlings are less frost-hardy than those of *N. attenuata,* it is likely that this germination behavior plays a role in determining the northern range limits of *N. trigonophylla.*

Water relations of mature plants

Phenological aspects.—A brief discussion of the effects of drought on the phenology of the desert tobaccos will serve as an introduction.

When overtaken by water stress at an early stage in growth, both species maintain a markedly excurrent growth form; the rosette leaves and lower cauline leaves quickly desiccate, while the upper leaves become more membraneous and are held in ascending fashion, enclosing the terminal bud. The ascending leaf habit also occurs in certain varieties of *N. tabacum,* and may play a role in reducing transpiration (Bliss *et al.* 1957). If the plants have not reached the flowering stage when water stress begins, flowering is soon initiated, even if the plant is only a few inches high. Fruiting progresses rapidly with drought, and the flowers become fewer and smaller, until flower buds cease forming altogether.

At one dry wash station in the Larrea desert (in the Virgin River drainage at 3,000 feet elevation, near Leeds, Utah), numerous small, incompletely developed individuals of *N. attenuata* and *N. trigonophylla* were growing in intimate association in 1957. In early June, the plants were assuming the drought condition described above, but both species were faring about equally. By August, however, the green leaves of *N. trigonophylla* were conspicuous among the mass of dry brown stalks of *N. attenuata,* which had succumbed to the summer drought. Since the plants of both species were rooted to the same depth and were growing side by side at this site, this is evidence for greater drought tolerance in *N. trigonophylla.*

Plants growing on moist sites pass through the same excurrent growth stage but soon become much branched by proliferation and growth of lateral buds. Many of these branches eventually rival the main leader, which appears to grow more slowly; hence, the plants develop a bushy, often rounded appearance. They bear an abundance of flowers, and often maintain the rosette leaves in green condition, while the upper leaves are horizontally disposed. If drought overtakes such fully developed plants, flowering quickly wanes, and the capsules ripen. Meanwhile, the foliage withers in acropetal progression. This happens very rapidly with *N. attenuata* (an annual) and the plants may desiccate completely within a few days. On the other hand, the suffrutescent *N. trigonophylla* (a facultative perennial) usually maintains a scattering of small green leaves and leafy buds along the withered branches during the drought period. This is additional evidence that *N. trigonophylla* is more drought tolerant than *N. attenuata.*

While considering the effect of water stress on phenological events, the vespertine flowering habit may be mentioned. In *N. attenuata* (but not in *N. trigonophylla*), the corollas expand in the evening and wilt in the rays of the hot morning sun. This habit is frequent in the arid and subarid West among members of diverse families, *e.g.,* Nyctaginaceae, Cactaceae, Onagraceae, Solanaceae. It was observed that if *N. attenuata* were growing on a site with morning shade, the flowers closed tardily, and with afternoon shade, opened precociously. One population situated next to an irrigation ditch had a few plants growing in tongues of visibly moist soil extending outward from the ditch. In the morning, these plants maintained the corolla limb in an expanded condition for several hours after the flowers of the rest of the population, on drier soil, had closed. It seems likely that the opening and closure of the perianth in vespertine plants is controlled, in part, by the environmentally affected turgidity of the tissues involved.

Relative turgidity.—Field measurements of the relative turgidity of populations of tobaccos growing in diverse environments were carried out, using the method of Weatherley (1950). The concept is defined as follows:

$$\text{relative turgidity} = \frac{\text{fresh weight} - \text{dry weight}}{\text{turgid weight} - \text{dry weight}} \text{ X } 100$$

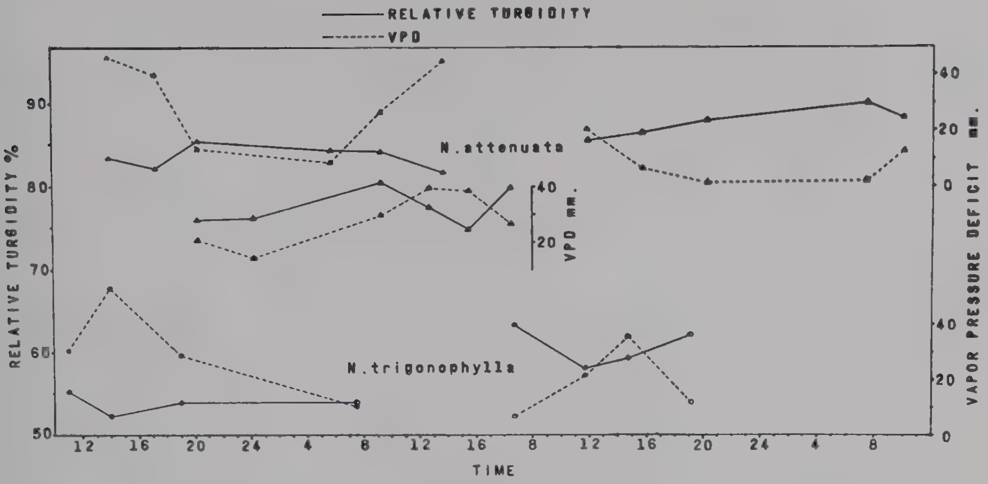


FIG. 8. The daily march of apparent relative turgidity in different populations of *N. attenuata* and *N. trigonophylla.*

For one observation, 60 leaf discs, each 7 mm. in diameter, were excised from mature leaves toward the base of the plants. The rosette leaves and lowermost cauline leaves were not used, because they were usually partly wilted or desiccated; several adjacent plants were necessary to procure a sufficient number of discs from leaves of similar position. The sampling was done as a series of pairs, symmetrically disposed with respect to the mid-rib, avoiding the leaf veins. One member of each pair, or a total of 30 discs, was used for dry weight determinations. The other 30 discs were collected in small, stoppered bottles, the fresh weight was recorded, and then the discs were floated for 20 hours on water in petri dishes, which were kept in a cool place. The turgid discs were blotted with filter paper to remove external water, placed in the bottles and weighed again to determine the turgid weight. To obtain the dry weight, the turgid discs were placed in brown envelopes and exposed to the desert air and sun for a few days, along with the 30 discs set aside for initial dry weight. The dry weights achieved following this treatment were not significantly different from oven-dry weights of the same discs, measured later in the laboratory.

A number of 24 hour relative turgidity cycles were carried out for each species during July and August, 1957, and these are presented graphically in Figure 8; all the cycles are plotted on the same ordinate (relative turgidity as per cent) for comparison. Each cycle represents a different site, but all were taken within a circle of 3.5 mile radius around Leeds, Washington Co., Utah, at altitudes ranging from 3,000 to 6,000 feet.

Though all the cycles show an inverse relation of relative turgidity to vapor pressure deficit, what is noteworthy is that the variation in relative turgidity on a 24-hour basis at any one site is small, compared to the variation among different sites.

The three *N. attenuata* cycles were all in a much higher relative turgidity range than the two *N. trigonophylla* cycles. The differences among these may be correlated with habitat differences; a brief description of these habitats illustrates the point.

Beginning with the *N. attenuata* cycles, the one depicted on the upper left in Figure 8 was taken from a population growing in a wash at 3,000 feet (Larrea zone). The plants were situated on a sandbar subjected to occasional lateral irrigation from small floods caused by heavy rains on the nearby Pine Valley Mountains (*ca.* 10,000 feet in elevation). Despite the very high vapor pressure deficits encountered every day, the plants maintained a high relative turgidity, retained their rossette leaves, and continued to grow and flower all summer long.

The cycle shown just below the former was taken from a population growing in disturbed ground along a pipe line at 4,600 feet (pinyon zone). Though higher in elevation, this habitat was drier than the last, since it received all of its water as precipitation. As the summer progressed, most of the rosette leaves and a few whole plants became desiccated at this site.

The third *N. attenuata* cycle, shown on the upper right, was obtained from a small population at about 6,000 feet (Gambel oak zone), growing on a bull-dozed mound of alluvium situated down-

TABLE VIII. Relative turgidity of *Nicotiana* leaves in relation to habitat factors

	Relative Turgidity	V.P.D. (mm.)	Air Temp. Shade (°F)	Substratum	Remarks	Elevation	Surrounding Vegetation	Date
N. trigonophylla	70.3%	24.4	89°	alluvial terrace	watered daily	3000′	*Larrea*	8-26
	58.0	21.1	86°	sandstone ledge	afternoon-shade	3000′	*Coleogyne*	8-26
	54.8	38.4	96°	basalt talus	S.W. facing	3600′	*Larrea*	8- 6
	52.2	26.4	90°	basalt talus	S. facing	4900′	*Coleogyne*	8- 6
	52.2	53.3	109°	wash alluvium	dry site	3000′	mesquite	8-18
N. attenuata	91.3	27.9	94°	irrigated sandbar	moist site, full sun	3000′	mesquite-*Chilopsis*	8-13
	89.5	23.3	90°					8- 5
	87.0	34.0	94°					8- 7
	83.0	32.4	94°					7-25
	82.3	40.1	101°					8- 2
	85.6	20.8	85°	bulldozed slope, wet by springs	N. facing	6000′	birch-aspen	8-11
	79.9	30.7	92°	bulldozed alluvium	sandy, full sun	4200′	evergreen chaparral	8- 7
	74.8	19.3	85°					8- 5
	70.8	17.2	82°					8-13
	78.3	36.8	95°	bulldozed alluvium	earthpile	3000′	*Larrea*	7-20
	74.9	38.6	98°	bulldozed alluvium	full sun	4600′	evergreen chaparral	7-15
	74.7	15.0	80°	dirt roadside	full sun	5100′	evergreen chaparral	8- 5
	74.5	29.5	91°					8- 7
	74.3	28.2	93°	deep sand	full sun	4200′	evergreen chaparral	8-14
	72.1	15.8	80°	dirt roadside	full sun	6200′	Gambel oak	8- 5
	69.5	24.9	86°					8- 7
	64.2	30.7	94°	wash alluvium	dry site	3000′	mesquite	7-25
	60.4	23.9	87°					7-15

slope from some large springs, which kept the whole site constantly moist. Some of the nearby deciduous trees cast afternoon shadows on the tobacco site. Despite the much reduced vapor pressure deficit, the relative turgidity cycle for this population was only slightly higher in level than that for the moist sandbar population down in the desert wash.

The two cycles shown for *N. trigonophylla* were taken about a mile apart at about 3,000 feet (Larrea zone). The one on the left was from a population growing in a dry wash less than a hundred yards from the moist sandbar population of *N. attenuata,* but was not reached by any flood waters in the summer of 1957. The right-hand cycle was obtained from a small population growing under a sandstone ledge, which cast an afternoon shadow on the plants.

In addition, a number of individual relative turgidity observations were made on tobacco populations growing in different habitats in the same general area. These observations were all taken during the heat of the day, mostly in the early afternoon, and are presented in Table VIII, together with the relative turgidity minima from the five 24-hour cycles. The data are arranged in descending order of relative turgidity, and all the readings from any one site are grouped together.

Table VIII shows that there is no consistent increase in relative turgidity with altitude, despite the general decrease in vapor pressure deficit. In fact, one of the lowest relative turgidity observations made for *N. attenuata* was on a dusty roadside at 6,200 feet elevation (Gambel oak zone), while the highest was on the moist sandbar at the desert elevation (3,000 feet, Larrea zone).

Very low relative turgidity levels were consistently found for *N. trigonophylla,* except for the one colony which was purposely watered (daily in June and July, every other day in August). These low values were associated with a complete cessation of growth and flowering and a gradual desicca-

TABLE IX. Changes in leaf water content and dry weight over a 24-hour period

Time of day	VPD, mm.	FW, mg.	DW, mg.	Field water content, mg.	Turgid water content, mg.	Relative turgidity per cent	Field water content, FW basis, per cent	Field water content, DW basis, per cent
2:00 PM (8-2-'57)	46.7	677	106	571	683	83.5	84.3	539
5:20 PM	40.1	654	104	550	669	82.3	84.0	530
8:15 PM	13.7	667	95	572	669	85.5	85.6	601
5:45 AM (8-3-'57)	8.6	579	82	497	589	84.4	85.8	605
9:15 AM	26.9	653	96	557	661	84.2	85.2	580
1:45 PM	45.0	686	101	585	708	82.5	85.3	580

tion of the larger leaves, even in the watered plant. This last was certainly unexpected; the only observed benefit to the watered plant was that it held more of its leaves in a green condition. Apparently these populations entered a summer dormancy which was not to be broken by merely providing more water. Seemingly contradictory to this were a few plants of this species found at moderate elevations (4,500 to 5,000 feet) and one small plant growing at 3,000 feet on ground wet by runoff from a spring, all of which continued to produce new growth and flowers all summer. Probably the dormancy on the less favored sites was drought-induced, and had commenced before the watering regime was begun.

The minimum relative turgidity level encountered for *N. trigonophylla* (52%) was lower than that found for *N. attenuata* (60%). Moreover, all of the *N. trigonophylla* populations measured were in the range of 52 to 63%, while most *N. attenuata* populations were in the range of 70 to 90% relative turgidity. This is further evidence for the greater desiccation tolerance of *N. trigonophylla*.

An analysis of the data from which the 24-hour cycles of relative turgidity were computed proved to be instructive; the *N. attenuata* cycle on the upper left in Figure 8 will be discussed in detail. The fresh weight (FW), dry weight (DW) and field water content of the 30 leaf discs (from the lower cauline leaves) are presented in Table IX for each sampling time, along with the relative turgidity and water content on both the fresh weight and the dry weight basis, and the vapor pressure deficit (VPD) of the atmosphere.

Two patterns are evident which suggest the existence of a causal interrelation: the dry weight cycle and the field water content cycle. The dry weight was highest in the afternoon and lowest at dawn, which is explicable in terms of diurnal photosynthesis versus nocturnal respiration and export of solutes without replenishment. The absolute water content of the discs was also highest in the afternoon and lowest at dawn, which is in contrast to both the relative turgidity and the water contents computed on the fresh weight and dry weight bases. Since these measurements were taken from leaves on the lower part of the stems, the following interpretation seems plausible. During the night, solutes are translocated from the older leaves up to the younger herbage and down into the roots, and in addition, there is some respiratory loss. This loss of solute lowers the osmotic concentration of the cell sap in the lower leaves, and their water balance is decreased by an internal shift of water in the plant (in response to a diffusion pressure deficit gradient) from the older to the younger leaves. During the day, photosynthesis in the older leaves may increase the osmotic concentration of their cell sap to an extent that better enables them to compete with the younger leaves for water. This may explain the peak in absolute water content in the lower leaves in the afternoon, despite the higher atmospheric vapor pressure deficit prevalent at this time.

Relative turgidity is computed partly on a basis of water content at full turgidity, which depends on the osmotic concentration of the tissues involved: the higher the osmotic concentration in the leaf discs, the greater the fully turgid weight can be. As a result of photosynthesis at high temperatures in intense sunlight, there may be a local accumulation of solutes in the leaves such that osmotic equilibrium is not achieved at the time the leaf discs are isolated for measurement. These discs, when floated on water, will imbibe to an extent that will give them a turgid weight much greater than their fresh weight, and hence a low apparent relative turgidity. The disparity between turgid weight and fresh weight will be less at night, when the osmotic concentration of the leaves is lower, and this will contribute toward the higher apparent relative turgidity at night. That a significant decrease in the fully turgid weight accompanies the reduction in dry weight at night is indicated by the data in Table IX. At dawn, the water content at full turgidity had decreased by 119 mg. or about 17 per cent below the afternoon maximum, while the dry weight had decreased by 24 mg. or about 23 per cent below the afternoon maximum.

The relative turgidity cycles in Figure 8 were plotted along with vapor pressure deficit to show the relation between the two, but it seems that their inverse relation may be at least partly due to coincidence in this case. At night, decreases occurred both in vapor pressure deficit and in dry weight. The slight apparent increase in relative turgidity was probably due mostly to the dry weight change, since the absolute water content actually decreased at night.

Since these effects are superimposed on the transpiration-induced turgidity cycle, the measurement of relative turgidity appears to have an equivocal basis, where differences of small magnitude are concerned.

Also, the water content on the dry weight basis is obviously greatly affected by dry weight changes. The apparent maximum in water content on the dry weight basis found at 5:45 A.M. (Table IX) is due entirely to the dry weight change, and not at all to an increase in absolute water content (the latter actually decreases). The fresh weight basis is likewise affected by significant dry weight changes, since fresh weight includes dry weight, and the magnitude of the dry weight change in this case was sufficient to create an apparent (but actually non-existent) increase in water content during the night, when interpreted on the fresh weight basis.

Thus, there appears to be no entirely satisfactory means for expressing water contents of plant tissues. The absolute water content of large, reproducible samples might be useful, but absolute water content is not in itself indicative of diffusion pressure deficit. Keeping in mind the fact that fluctuations in dry weight involving osmotically active solutes may affect the apparent relative turgidity as much as, or more than, variations in absolute water content due to the march of transpiration, relative turgidity remains as a useful indicator of diffusion pressure deficit of tissues, as was shown by Weatherley and Slatyer (1957).

To return again to field measurements of the water balance of desert tobaccos, consideration should be given to habitats in which the extremes of relative turgidity occurred. While *N. attenuata* reached its lowest relative turgidity (60%) on the dry wash site at an elevation of 3,000 feet (Larrea zone), it reached comparably low levels on dry sites at 6,000 feet (Gambel oak zone), where the daily vapor pressure deficit cycle is much less extreme. Moreover, one of the highest relative turgidity figures recorded for this species (91%) was from a periodically irrigated sandbar less than a hundred yards from the population with the 60% relative turgidity (both being located in the same wash at 3,000 feet). This illustrates the obvious effect of soil moisture on the relative turgidity of plants, which outweighs differences in atmospheric vapor pressure deficit correlated with altitudinal differences. However, it is probable that the lower potential evapotranspiration at the higher elevations, due to reduced temperature, permits the establishment of tobaccos on sites with a soil moisture stress that would be deleterious at higher atmospheric stresses.

This points to the necessity for a distinction between atmospheric drought and soil drought. The current view sometimes tends to emphasize atmospheric drought, measured in terms of potential evapotranspiration, as an important factor in determining plant distribution. While it is true that the higher the potential evapotranspiration, the more rapidly will a given soil moisture capital be depleted, the atmospheric dryness may be largely negated if a soil is periodically receiving additional moisture capital, or if the volume of moist soil permeated by the plant roots is sufficiently large. In arid regions soil climate is all-important.

Season of Flowering

An analysis of herbarium collections of the two species, in the institutions already cited, gave data on the frequency of flowering in different months of the year, which are presented in Table X.

TABLE X. Frequency of flowering in terms of monthly collections

Month	NUMBER OF COLLECTIONS	
	N. attenuata	*N. trigonophylla*
January	0	5
February	0	10
March	1	45
April	3	76
May	9	47
June	62	42
July	125	29
August	90	28
September	37	24
October	9	16
November	3	6
December	0	8
	339	336

The annual *N. attenuata* has been collected in flower during 9 months of the year, not being found in mid-winter, but the great majority of records is concentrated in the season from June to September, which is the driest part of the year in most of the *N. attenuata* range.

On the other hand, *N. trigonophylla,* a facultative perennial which may be evergreen in favorable sites, has been collected in flower in every month of the year. The winter records are by no means confined to the southern part of the range, for there are records for late December near the northern limits of the species. March to October appears to be the principal flowering season, however.

The Desert Tobacco Ecosystem

Tobaccos are often the only large, leafy green herbs to be seen in dry washes and other desert situations in the summer. As such, they serve as an oasis for a distinctive insect fauna. These insects may derive their entire sustenance from the tobaccos, and constitute with them a semi-autonomous ecosystem, related to larger ecosystems mainly by the incursions of a few predators.

The insects encountered on all populations studied in the field were collected, and most of the principal types were identified through Dr. J. F. Gates Clark of the United States National Museum. This fauna was remarkably constant on Nicotiana from Texas to Oregon, regardless of the species involved. A brief description of the insects and other animals associated with the desert tobaccos follows:

Herbivores.—These may be considered under three categories: a foliage fauna, a capsule fauna, and a floral fauna, the last including the pollinators.

Foliage fauna: *Protoparce quinquemaculata* (Haworth), tomato or tobacco hornworm. The caterpillars of this lepidopteran are voracious feeders, and may strip a plant of leaves in a short time. The adult moth was not observed as a pollinator for Nicotiana flowers.

Pronotacantha annulata (Uhler), stilt bug. This heteropteran, resembling a small daddy-longlegs with black-tipped antennae and spiny thoracic protuberances, has a remarkable ability to make its way through the sticky glandular hairs present on the herbage of tobaccos, especially *N. trigonophylla.* It presumably sucks plant sap, judging from the mouth-parts, although it could be predacious on other insects.

Capsule fauna: *Corimelaena virilis* (McA. & M.), negro bug. This is a small, black, beetle-like heteropteran, which sits on the ripening capsules until they begin to dehisce, then forces its way in through the apex and presumably feeds on the seeds, which are always light and sterile in infested capsules. The large number of nymphs and cast skins of this species which were found in Nicotiana capsules indicates that the entire life cycle may be completed there. When this bug is abundant, as is often the case, it causes a significant decrease in the reproductive potential of the tobaccos.

Floral fauna (pollinators): Pollination was observed only for *N. attenuata.* The animals involved are listed below:

Archilochus alexandri, black-chinned hummingbird.

Celerio lineata (F.) hawkmoth (larvae not observed on *Nicotiana*).

Halictus sp., sweat-bee.

Metasyrphus venablesi (Curran), syrphid fly.

Higher trophic levels (predators).—Small white spiders, which were not identified and may consist of more than one taxon, were ubiquitous among the white Nicotiana flowers throughout the West.

The *Protoparce* caterpillars were occasionally seen being eaten by certain lizards. These in turn are eaten by *Geococcyx californianus* (roadrunner), and the food-chain could be extended from here even more tenuously to various carnivorous animals which prey on roadrunners, among which may be bobcats, foxes, coyotes, and the raptores, Buteo, Aquila and Bubo.

DISCUSSION

The habitats of *Nicotiana attenuata* and *Nicotiana trigonophylla* may be grouped under three categories: bedrock outcrops and talus, beds of intermittent watercourses, and ruderal sites. In all three types, both species were found exclusively on coarse-textured soils, high in gravel and sand and low in clay. Although these three habitat categories appear somewhat heterogeneous and unrelated, they have, besides soil texture, two other things in common. First, they are all subject to continued disturbance due to the agency of erosion or man, and are therefore kept in an open, pioneer state, successionally speaking. Secondly, but at least equally important, they are all periodically favored in regard to the water factor, whether due to the watershed effects of rocks and road surfaces or to the sporadic floods in the dry wash habitat.

The significance of this ecological distribution appears to lie, in the first place, in a low capacity for competition on the part of the desert tobaccos, probably for water. Both species have an extensive, rather thinly cutinized leaf surface, and these are characters usually associated with a high water requirement.

By way of comparison, a summary of Nicotiana habitats in other parts of the range of the genus was made, insofar as the limited information permittted. I am indebted to N. T. Burbidge (personal communicaion, 1958), a botanist associated with the Commonwealth Scientific and Industrial Research Organization of Australia, for a concise account of the ecology of the genus on that continent. Most of the habitats of the Australian species fall into the same three major categories found for *N. attenauta* and *N. trigonophylla* and are arranged to illustrate this in Table XI.

TABLE XI. Ecology of the genus *Nicotiana* in Australia*

Species	Beds of intermittent watercourses	Bedrock outcrops and talus	Ruderal sites (roadsides, disturbed vegetation, etc.)	Shade of trees in open terrain
N. velutina	+			
N. exigua	+			
N. stenocarpa	+			
Nicotiana sp. nov. 1	+			
N. occidentalis	+			+
N. debneyi	+		+	
N. megalosiphon	+		+	+
N. rotundifolia	+	+	+	+
N. excelsior		+		
N. benthamiana		+		
N. gossei		+		
N. suaveolens		+		
Nicotiana sp. nov. 2		+		
N. ingulba				+

* Data from Burbidge (1958).

A tentative world-wide picture of the ecology of the genus Nicotiana was assembled from Goodspeed's monograph (1954) which includes brief remarks on the ecology of most species, and from Burbidge's account of the Australian species. Habitat information was available for 54 of the approximately 60 species in the genus. Watercourses (chiefly intermittent) harbored 36 species, bedrock outcrops and talus, 25, and ruderal sites (mostly roadsides), 20. Forty-eight species occurred in rocky or sandy soil, and 4 in fine-textured soil. This is not a complete listing of habitat types, but only those in which the genus occurs to an extent worth mentioning. It is evident that the genus Nicotiana, for the most part, is composed of pioneer species, which occupy disturbed sites with soils of coarse texture. The disturbance factor suggests a requirement for low competition pressure, while the soil texture indicates a high root aeration requirement. The roots of *Nicotiana tabacum* are known to require a well-aerated soil, for when subjected to conditions of inadequate drainage, such as in the low parts of a field, "flopping" (severe wilting of the tops) takes place (Kramer and Jackson 1954).

Perhaps the most outstanding adaptation of Nicotiana to the invasion of pioneer or disturbed sites is the mobility conferred by an enormous production of very minute seeds with rough reticulate coats. This provides great powers of dispersal whether due to the agency of wind or animals.

On the other hand, the small seed size carries with it the disadvantage of a small food reserve, which limits the depth of successful germination to the magnitude of the relatively small dark-elongation of the hypocotyl. Hence, much seed would be lost by dark germination following slight burial were it not for the fact that the seeds are light-requiring, which insures germination near the surface.[5] However, the soil-air interface is a harsh environment. As the center of radiation exchange, it undergoes the most rapid and extreme temperature changes, and with regard to the moisture factor, it is alternately bombarded by splattering raindrops and subjected to severe droughts. Therefore, any depth below the surface, however slight, will be an improvement from the standpoint of an environment for germination of seeds. If then, a seed is light requiring, it is of some survival value for it to be red sensitive, as is the case with the tobaccos, since this property will facilitate germination at nearly the maximum depth of penetration by visible light.

Hence, adaptations for seed dispersal and germination contribute to the weedy or pioneer character which epitomizes the ecology of Nicotiana.

SUMMARY

An ecological investigation was made of two species of the genus Nicotiana indigenous to the arid portions of western North America, *N. attenuata* Torrey and *N. trigonophylla* Dunal.

Nicotiana attenuata is primarily a cold desert species, being found chiefly in the Great Basin, while *N. trigonophylla* is restricted to the warm or subtropical deserts of the Southwest.

The habitats of the two species may be grouped under three categories: bedrock outcrops and talus, beds of intermittent watercourses, and ruderal sites. *N. trigonophylla* is most frequent in the first two, while *N. attenuata* is most frequent in the last.

These habitats have two things in common. First, they are all subject to continued disturbances due to the agency of erosion or man, and are therefore kept in a pioneer state, successionally

---

[5] It is probable that the soil disturbance factor in the environment of these tobaccos plays an important role in bringing buried seeds closer to the surface.

speaking. Secondly, they are all periodically favored in regard to the water factor, whether due to the watershed effects of rocks, road surfaces, etc., or to the sporadic floods in the dry wash habitat.

The mean granulometric composition was similar for the soils collected for the two species. Both species were found exclusively on coarse textured soils, high in gravel and sand, and low in clay.

The series of soil samples collected for both species showed a strong mode in the circumneutral pH range, and were mostly nonsaline.

Neither species is immediately associated with undisturbed vegetation in the sense of forming a synusial element within it. Rather, they occur enclave-wise on various disturbed, open sites. *N. attenuata* occurs in a wider range of vegetation types than *N. trigonophylla,* which is largely restricted to the more xeric types. The modal occurrence class for the former is northern or cold desert shrub, and for the latter, southern or warm desert shrub.

Seed germination of both species was strongly inhibited by solutions with osmotic concentrations of 11.8 atm. and above. However, at the 7.0 atm. level, *N. trigonophylla* was much less affected than *N. attenuata.* This correlates with the soil salinity data obtained in field studies; *N. trigonophylla* occurred on soils of higher salinity.

The seeds of *N. attenuata* (but not of *N. trigonophylla*) require stratification at 33°-40° F. before germination will take place. This constitutes an effective mechanism for preventing germination of seeds in summer, when seedling establishment would be precarious because of high temperatures and accompanying drought. The stratification requirement may also play a part in determining the southern limit of range for *N. attenuata,* since cold temperatures are essential to the process.

The seeds of both species were found to be capable of germinating under 9 inches of water. This property may have survival value in the dry wash habitat, where small pools of water persist, following floods. Submerged germination would afford protection during the critical establishment period against desiccation and killing frost, and insurance of a soil moisture reserve lasting well into the dry season.

Light was found to be required for seed germination of both species. The red end of the spectrum was most effective, and the blue end least, in promoting germination. Since it was found that the transmission of light by the seed coats was seven times greater in the red end of the spectrum than in the blue, this may largely account for the greater effectiveness of red light.

Transmission spectra of sand and of a clay suspension showed that light of longer wavelength would penetrate the soil deepest.

The light requirement insures germination near the surface, which is of survival value because of the small food reserve associated with the minute size of the seeds. On the other hand, the red light sensitivity permits the seeds to germinate in the more favorable environment at the maximum depth of penetration by visible light, since red light penetrates deepest.

Data are presented which show that the apparent fluctuation in relative turgidity in the lower leaves of *N. attenuata,* during a 24-hour period, was due less to changes in absolute water content than to dry weight changes involving materials which are presumably osmotically active.

A comparison of the relative turgidity levels of desert tobaccos growing in different habitats, at different elevations, showed the importance of microsite differences, presumably with respect to soil moisture, which outweighed differences in atmospheric vapor pressure deficit correlated with elevation.

Nicotiana attenuata and *N. trigonophylla* are pioneer plants of the desert, but not true xerophytes. They inhabit disturbed soils of coarse texture, situated in physiographic niches periodically favored with respect to the water factor, but free of dense vegetation. They are excellently adapted to the rapid invasion of such pioneer sites by virtue of the mobility conferred on them by an enormous production of very minute seeds.

References

Billings, W. D. 1949. The shadscale vegetation zone of Nevada and Eastern California in relation to climate and soils. Amer. Midl. Nat. **42**: 87-109.

Bliss, L. C., P. J. Kramer, and F. A. Wolf. 1957. Drought resistance in tobacco. Tobacco **145**: 20-23.

Bouyoucos, G. J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. Soil Sci. **42**: 225-228.

Goodspeed, T. H. 1954. The genus Nicotiana. Chronica Botanica, Waltham, Mass. 536 pp.

Kearney, T. H. and R. H. Peebles. 1951. Arizona Flora. Univ. of Calif. Press, Berkeley, Calif. 1032 pp.

Kramer, P. J. and W. T. Jackson. 1954. Causes of injury to flooded tobacco plants. Plant Physiol. **29**: 241-245.

Lebedeff, A. F. 1928. The movement of ground and soil waters. Proc. Intern. Congr. Soil Sci., 1st Congr. **1**: 459-494.

Richards, L. A. 1947. Pressure membrane apparatus construction and use. Agr. Engin. **28**: 451-454.

———. 1948. Porous plate apparatus for measuring moisture retention and transmission by soil. Soil Sci. **66**: 105-110.

———, editor. 1954. Diagnosis and improvement of saline and alkali soils. U. S. Department of Agriculture. Agric. Handb. No. **60**. 160 pp.

Toole, E. H., S. B. Hendricks, H. A. Borthwick, and Vivian K. Toole. 1956. Physiology of seed germination. Ann. Rev. Plant Physiol. **7**: 299-324.

Weatherley, P. E. 1950. Studies in the water relations of the cotton plant. I. The field measurement of water deficits in leaves. New Phytol. **49**: 81-97.

——— **and R. O. Slatyer.** 1957. The relationship between relative turgidity and diffusion pressure deficit in leaves. Nature **179**: 1085-1086.

THE CHEMICAL CONTENT IN VARIOUS PORTIONS OF THE CURRENT GROWTH OF SALT-DESERT SHRUBS AND GRASSES DURING WINTER

C. Wayne Cook, L. A. Stoddart, and Lorin E. Harris[1]
Utah Agricultural Experiment Station, Logan, Utah

Introduction

It is generally believed that as a range plant is more intensely utilized, the nutritional value of the ingested material decreases. Ordinarily, animals first consume stem tips and small twigs; with increased utilization they consume the stem toward the base. As utilization increases, animals consume more and more stemmy material and less leafy material (Cook *et al.* 1953). Under heavy use, the bases of the stems are consumed (Figs. 1 and 2).

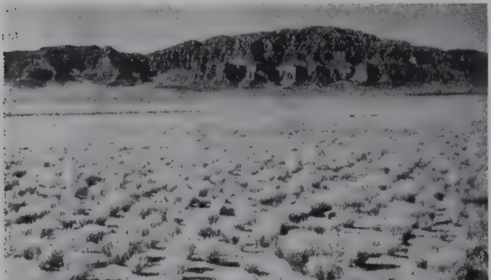


Fig. 1. A pure stand of winterfat early in the winter grazing season with only light utilization.

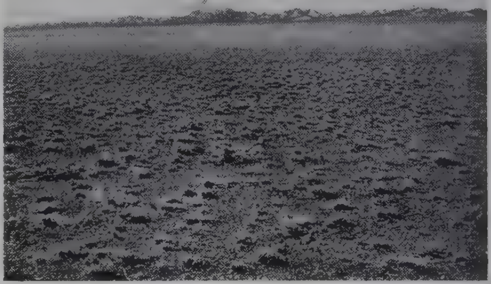


Fig. 2. A pure stand of winterfat late in the winter grazing season after being grazed several times. During the last grazing, animals consumed considerable quantities of the basal stem material.

There is little information dealing with the chemical content of the tips of stems compared to lower portions. Aldous (1945) found that twigs of bitterbrush (*Purshia tridentata*), clipped at short lengths, contained more protein, fats, and carbohydrates than twigs cut at longer lengths. Hardison *et al.* (1957) found that the dry matter in the bottom portion of the alfalfa plant was only 87% as digestible as that in the top portion. As the stage of growth advanced, the digestibility of dry matter in the base decreased at the rate of 0.6% per day, but the digestibility of the top remained unchanged.

The present study in west central Utah was designed to determine the chemical content of the various portions of the past summer's growth in common salt-desert plants during the winter dormant period.

Seven shrubs and four grasses were selected: black sage (*Artemisia nova*), winterfat (*Eurotia lanata*), desert molly (*Kochia vestita*), Mormon tea (*Ephedra nevadensis*), four-wing saltbush (*Atriplex canescens*), yellowbrush (*Chrysothamnus stenophyllus*), shadscale (*Atriplex confertifolia*), needle-and-thread grass (*Stipa comata*), galleta grass (*Hilaria jamesii*), sand dropseed (*Sporobolus cryptandrus*), and Indian ricegrass

---

[1] Research Professor, Professor and Head of Department of Range Management, and Professor of Animal Husbandry, respectively. The authors are indebted to David Williamson for chemical analysis of plant material and to Dicky Turner for his assistance in collecting plant material.

TABLE I. Average chemical content of the current year's growth of eleven dominant salt-desert plants harvested at six dates during the winter grazing season from two locations on a dry basis

Species	Date	Ether extract	Total protein	Ash	Lignin	Cellulose	Other carbohydrates	Phosphorus	Calcium	Gross energy
					(percent)					(Cal/gm.)
Black sagebrush	Oct. 26	7.3	8.0	4.3	14.8	19.3	46.3	.13	.60	4.95
	Nov. 26	5.3	7.2	5.0	14.6	20.9	40.5	.10	.67	4.92
	Dec. 26	5.4	6.9	4.3	14.6	23.2	45.6	.10	.64	5.03
	Jan. 26	6.1	8.5	5.3	17.1	18.7	44.4	.13	.88	4.92
	Feb. 24	5.4	6.2	3.7	17.9	26.0	40.8	.07	.67	4.81
	Mar. 31	5.5	6.9	4.3	15.1	24.0	44.2	.12	.74	4.81
	Average	6.0	7.3	4.5	15.7	22.0	44.7	.11	.70	4.91
Winterfat	Oct. 26	3.3	10.4	10.1	12.3	19.3	44.6	.08	1.89	4.17
	Nov. 26	2.7	8.3	8.5	16.3	22.4	41.8	.07	1.79	4.51
	Dec. 26	2.3	8.0	9.8	14.5	23.7	41.7	.09	1.83	4.22
	Jan. 26	2.2	8.4	9.9	13.7	23.2	42.7	.08	1.90	4.18
	Feb. 24	2.4	8.0	9.2	16.8	21.6	42.0	.09	1.79	4.21
	Mar. 31	2.0	8.2	8.6	19.2	21.5	40.6	.09	1.44	4.40
	Average	2.5	8.5	9.4	15.5	22.0	42.2	.08	1.78	4.28
Desert molly	Oct. 26	2.0	11.5	15.5	12.2	15.7	42.9	.07	1.24	3.94
	Nov. 26	1.7	9.1	13.7	13.1	18.9	43.7	.06	1.61	4.10
	Dec. 26	1.5	9.1	12.2	14.7	20.1	42.5	.07	1.52	4.22
	Jan. 26	1.4	8.7	11.1	15.2	21.9	41.7	.06	1.90	4.22
	Feb. 24	1.3	8.9	10.5	15.8	21.7	41.9	.06	1.79	4.20
	Mar. 31	1.4	8.6	10.0	16.7	20.1	43.2	.22	1.17	4.20
	Average	1.6	9.3	12.2	14.6	19.7	42.7	.09	1.42	4.15
Mormon tea	Oct. 26	3.1	8.9	5.9	18.2	25.7	38.3	.09	1.72	4.60
	Nov. 26	4.1	7.9	4.7	16.2	26.1	41.1	.09	1.93	4.68
	Dec. 26	2.9	7.3	5.4	19.0	26.1	39.3	.09	1.96	4.66
	Jan. 26	3.7	7.4	5.6	20.0	26.0	36.9	.09	2.09	4.46
	Feb. 24	3.7	7.2	4.6	18.2	26.5	39.9	.09	1.54	4.45
	Mar. 31	3.0	7.3	4.9	19.1	26.3	39.4	.10	1.97	4.60
	Average	3.4	7.6	5.2	18.4	26.1	39.2	.09	1.87	4.57
Four-wing saltbush	Oct. 26	4.3	12.1	13.2	10.5	16.5	44.9	.11	1.52	4.21
	Nov. 26	3.1	9.9	10.8	11.8	20.3	44.2	.09	1.58	4.43
	Dec. 26	2.5	10.0	11.7	12.2	20.5	43.1	.11	1.52	4.51
	Jan. 26	2.2	9.9	10.9	12.7	23.3	41.0	.10	1.53	4.43
	Feb. 24	2.3	9.7	10.3	12.8	22.1	42.8	.10	1.34	4.42
	Mar. 31	1.9	9.5	9.9	13.4	25.4	40.0	.10	1.43	4.47
	Average	2.7	10.2	11.1	12.2	21.3	42.7	.10	1.49	4.41
Yellowbrush	Oct. 26	12.5	10.1	8.2	10.4	13.3	45.5	.13	1.95	5.11
	Nov. 26	14.9	8.5	8.8	10.9	14.6	42.2	.10	1.79	4.96
	Dec. 26	12.7	7.7	8.8	12.4	15.8	42.6	.11	2.09	4.83
	Jan. 26	11.1	7.3	8.1	13.4	18.6	40.2	.10	2.01	5.01
	Feb. 24	11.5	7.5	7.3	13.1	17.1	43.5	.10	2.04	4.89
	Mar. 31	8.8	9.6	8.4	13.5	16.0	43.7	.13	1.97	4.81
	Average	11.9	8.5	8.3	12.3	15.9	43.0	.11	1.98	4.93

(*Oryzopsis hymenoides*). Each was harvested at four intensities: 0-25, 26-50, 51-75, and 76-100%. Harvesting was done each month from October 26 to March 31 at two different locations. The intensities of harvesting were based largely upon length of current growth, but were adjusted somewhat to approach equal weight for each 25% increment. Thus the 0-25% included only the tips of stems, whereas 76-100% included the lowermost portion. The four intensities are presented—for purposes of discussion—as light, moderate, heavy, and very heavy. The six harvesting dates were selected to represent the normal winter grazing period on salt-desert ranges of the intermountain area.

RESULTS AND DISCUSSION

Observations made during midwinter revealed the presence of green material in most species.

Needle-and-thread grass, Indian ricegrass, and —to a limited extent—sand dropseed were somewhat green and tough at the bases of the seed culms. The basal portions of the vegetative stems or seedless culms were dark green and succulent. All culms and leaves were dry and brittle at the tips. Galleta grass was dry and brittle throughout.

Desert molly and winterfat were dry and brittle at the tops, but the stem bases were green and tough. Buds at the stems bases were not open, but were green and slightly swollen. The seed culms of yellowbrush were similar, but vegetative

TABLE I. (Continued)

Species	Date	Ether extract	Total protein	Ash	Lignin	Cellulose	Other carbohydrates	Phosphorus	Calcium	Gross energy
Shadscale	Oct. 26	2.6	9.9	17.5	15.1	17.9	36.8	.08	2.42	4.01
	Nov. 26	2.1	9.4	16.9	14.0	20.1	37.6	.10	1.83	4.13
	Dec. 26	2.1	9.9	17.8	14.9	16.0	39.9	.09	1.84	4.11
	Jan. 26	3.6	8.6	15.8	16.8	20.7	36.2	.08	1.32	4.21
	Feb. 24	2.0	7.0	12.2	15.8	22.2	40.9	.07	1.48	4.15
	Mar. 31	2.0	6.4	10.2	17.3	22.6	41.5	.07	1.45	4.24
	Average	2.4	8.5	15.1	15.7	19.9	38.8	.08	1.72	4.14
Needle-and-thread grass	Oct. 26	2.5	4.1	9.0	7.9	36.3	40.1	.05	.61	4.17
	Nov. 26	2.5	4.1	9.0	7.6	37.8	39.0	.05	.61	4.21
	Dec. 26	2.0	3.3	9.3	7.9	38.3	40.5	.05	.61	4.19
	Jan. 26	2.7	3.3	9.9	8.1	38.5	37.5	.05	.67	4.11
	Feb. 24	2.2	3.6	11.8	8.1	37.2	37.1	.05	.93	4.03
	Mar. 31	1.9	5.3	8.9	8.4	35.9	39.7	.07	.88	4.13
	Average	2.3	3.9	9.6	8.0	37.3	39.0	.05	.72	4.14
Galleta grass	Oct. 26	2.0	4.5	12.9	8.1	29.7	42.7	.06	.61	3.93
	Nov. 26	1.8	4.3	12.8	7.2	31.4	42.5	.07	.97	3.98
	Dec. 26	1.4	4.2	13.2	8.1	30.5	42.7	.13	.77	3.95
	Jan. 26	1.5	3.3	15.9	8.7	30.2	39.0	.06	.86	3.81
	Feb. 24	1.4	3.5	14.1	8.7	31.5	40.9	.06	.78	3.84
	Mar. 31	1.2	3.3	14.3	8.3	30.7	42.2	.07	.77	3.86
	Average	1.6	3.9	13.9	8.2	30.7	41.7	.07	.84	3.89
Sand dropseed	Oct. 26	1.0	5.0	8.0	8.7	40.4	36.9	.05	.53	4.07
	Nov. 26	1.3	4.6	8.0	8.3	40.0	37.8	.06	.80	4.21
	Dec. 26	.9	4.4	8.4	8.2	40.7	37.4	.05	.59	4.16
	Jan. 26	1.1	3.9	8.3	8.5	41.7	36.6	.06	.61	4.10
	Feb. 24	1.2	3.5	9.2	8.3	42.0	36.8	.05	.76	4.04
	Mar. 31	1.1	3.1	8.5	8.0	39.8	38.5	.07	.62	4.04
	Average	1.1	4.1	8.4	8.3	40.8	37.3	.06	.65	4.10
Indian ricegrass	Oct. 26	2.1	5.3	9.4	8.4	34.3	40.5	.04	.90	4.24
	Nov. 26	1.7	4.9	9.9	8.4	34.3	40.9	.04	.82	4.18
	Dec. 26	1.2	4.0	10.1	8.8	35.4	40.5	.04	.78	4.19
	Jan. 26	1.3	4.0	9.0	8.5	35.0	42.2	.04	.77	4.15
	Feb. 24	1.0	3.9	8.8	9.4	35.9	41.0	.04	.79	4.20
	Mar. 31	1.2	5.7	8.2	9.2	34.4	41.6	.06	.73	4.17
	Average	1.4	4.6	9.2	8.8	34.9	41.2	.04	.80	4.19
Averages for various dates of harvesting	Oct. 26	3.9	8.2	10.4	11.5	24.4	41.8	.08	1.30	4.31
	Nov. 26	3.9	7.1	9.8	11.7	26.1	41.6	.08	1.31	4.39
	Dec. 26	3.2	6.8	10.1	12.3	26.4	41.4	.08	1.29	4.37
	Jan. 26	3.4	6.6	10.0	13.0	27.1	40.0	.08	1.28	4.33
	Feb. 24	3.1	6.3	9.2	13.2	27.6	40.7	.07	1.24	4.30
	Mar. 31	2.7	6.7	8.8	13.5	27.0	41.3	.10	1.20	4.34

stems had swollen green buds over their entire length. These stems were shorter than seed-bearing stems, so that the greener material was still confined largely to the base of the plant. Black sage seed stems were greener at the bases, and green leaves were more abundant at the bases of the stems, so close clipping resulted in harvest of greener and leafier material. Conversely, four-wing saltbush appeared to be more leafy at the stem tip, and branching twigs were more numerous and finer in texture. Stems toward the bases were larger and coarser, with fewer leaves. Both base and apex of young twigs appeared to be equally green, but the upper portion was more succulent. In the fall the seed was abundant at the apex, but a large portion was shattered. Shadscale had more leafy and succulent material at the stem tips than at the woody bases. Buds were open the entire length of the stem, but they were more plentiful from the mid-section upward.

A more detailed description of the appearance of these desert plants was given by Cook *et al.* (1954).

Chemical Analysis

The average chemical content of the current year's growth at various dates is shown in Table I, and each intensity of harvesting for each species is shown in Table II. Changes in chemical content for some of the important constituents for selected species are presented in Table III to show some of the important interactions between species, dates, and intensities.

Table II. Average chemical content of eleven dominant salt-desert plants harvested at four intensities during the winter grazing season from two locations on a dry basis

Species	Intensity	Ether extract	Total protein	Ash	Lignin	Cellulose	Other carbohydrates	Phosphorus	Calcium	Gross energy
					(percent)					(Cal/gm)
Black sagebrush	0-25	5.4	7.1	4.0	15.1	21.5	48.0	.09	.65	4.85
	26-50	6.2	7.2	4.3	15.7	22.4	44.1	.11	.70	4.95
	51-75	6.1	7.4	4.9	16.0	22.0	43.5	.12	.67	4.94
	76-100	8.3	8.4	4.8	16.9	22.8	38.8	.13	.92	4.91
Winterfat	0-25	2.1	7.9	9.4	12.7	22.7	45.2	.07	2.08	4.17
	26-50	2.5	9.3	9.0	15.2	22.4	41.6	.09	1.65	4.35
	51-75	2.8	8.8	8.5	18.7	21.7	39.6	.09	1.49	4.44
	76-100	2.9	9.3	8.9	20.2	18.7	40.0	.09	2.34	4.50
Desert molly	0-25	1.6	8.9	12.4	11.8	21.3	44.1	.05	1.46	4.12
	26-50	1.6	9.0	11.8	14.8	18.8	44.0	.06	1.35	4.14
	51-75	1.6	9.9	11.9	17.0	19.7	40.0	.08	1.38	4.21
	76-100	1.2	10.1	12.0	17.5	17.7	41.5	.09	1.69	4.10
Mormon tea	0-25	3.4	8.0	5.7	18.0	26.4	38.4	.09	1.91	4.54
	26-50	3.6	7.8	5.1	17.6	26.0	39.9	.09	1.97	4.56
	51-75	3.3	7.5	4.9	19.6	25.7	38.9	.08	1.84	4.62
	76-100	3.0	5.8	4.4	19.8	26.0	41.0	.09	1.28	4.68
Four-wing saltbush	0-25	2.7	12.0	13.7	9.9	15.7	46.0	.12	1.75	4.42
	26-50	3.5	10.7	11.5	11.8	20.1	43.5	.10	1.51	4.42
	51-75	2.6	9.0	10.0	14.2	23.3	40.9	.10	1.46	4.40
	76-100	2.9	9.0	9.3	16.4	26.3	36.0	.09	1.20	4.40
Yellowbrush	0-25	13.8	7.3	8.3	10.0	16.6	44.0	.10	1.92	5.01
	26-50	12.6	9.5	7.9	12.3	15.9	41.7	.12	1.86	5.00
	51-75	9.5	9.0	8.1	14.6	16.0	42.9	.12	2.01	4.87
	76-100	11.6	9.6	10.9	14.3	12.1	41.5	.11	2.61	4.52
Shadscale	0-25	3.0	9.0	15.6	14.8	20.7	38.5	.08	1.75	4.13
	26-50	2.2	8.7	15.9	15.9	18.6	38.9	.09	1.73	4.08
	51-75	2.2	8.2	14.6	16.3	20.0	38.5	.09	1.67	4.17
	76-100	1.9	7.0	11.8	17.4	20.3	41.6	.08	1.81	4.34
Needle-and-thread grass	0-25	2.2	3.4	6.9	7.5	39.3	40.8	.04	.68	4.25
	26-50	2.3	3.8	9.5	8.0	38.0	39.2	.05	.61	4.17
	51-75	2.4	4.4	12.0	8.3	34.6	38.4	.07	.88	4.04
	76-100	2.3	5.1	12.3	9.1	35.0	36.2	.06	.68	3.98
Galleta grass	0-25	1.5	4.0	11.2	7.8	33.0	42.4	.06	.64	3.97
	26-50	1.6	4.0	12.3	8.0	31.2	42.8	.06	.72	3.97
	51-75	1.5	3.9	15.1	9.3	29.6	40.4	.06	.88	3.83
	76-100	1.9	2.8	16.8	8.8	28.7	41.0	.10	1.63	3.49
Sand dropseed	0-25	.9	4.5	5.7	8.1	43.6	37.1	.06	.67	4.24
	26-50	1.0	3.9	7.7	8.0	41.9	37.6	.06	.57	4.10
	51-75	1.2	3.8	10.4	8.4	38.8	38.0	.05	.70	4.09
	76-100	1.8	3.8	15.1	10.2	34.0	35.1	.04	.86	3.49
Indian ricegrass	0-25	1.5	4.4	8.5	7.3	34.7	43.6	.04	.81	4.21
	26-50	1.4	4.5	9.0	9.1	36.1	40.0	.04	.66	4.18
	51-75	1.2	4.8	9.1	10.0	34.6	40.4	.05	.78	4.18
	76-100	1.5	5.3	13.6	10.8	31.5	37.3	.06	1.50	4.15
Averages for intensity of utilization	0-25	3.5	6.9	9.2	11.2	26.9	42.6	.07	1.30	4.35
	26-50	3.5	7.1	9.5	12.4	26.5	41.2	.09	1.21	4.36
	51-75	3.1	7.0	10.0	13.9	26.0	40.1	.08	1.25	4.35
	76-100	3.0	6.8	12.0	14.9	25.7	37.6	.08	1.48	4.14

The statistical analysis of data is presented in Table IV.

Considerable difference in chemical content was found among species, and the content of various portions within each species varied widely. Likewise, the change in chemical content during various time periods was markedly different among the various species.

Ether extract.—The ether extract content varied significantly among species. Browse species had higher values than grasses; species high in essential oils, such as black sage and yellowbrush,

TABLE III. Average chemical content of two grasses and two shrubs during three periods for four clipping intensities

		DATES											
		October 26				January 26				March 31			
Species	Intensity	Total protein	Lignin	Cellulose	Ash	Total protein	Lignin	Cellulose	Ash	Total protein	Lignin	Cellulose	Ash
		(percent)				(percent)				(percent)			
Sand dropseed grass	0-25	5.8	8.7	43.2	4.6	4.3	7.6	45.0	5.3	2.7	7.0	42.8	5.8
	26-50	4.7	8.6	42.0	7.5	3.7	8.0	42.7	7.9	3.1	7.6	40.8	7.7
	51-75	4.7	8.2	38.9	10.4	3.8	9.2	41.8	9.6	2.6	8.9	36.9	10.4
	76-100	3.9	10.5	26.2	15.1	3.1	11.9	41.2	15.6	6.4	10.6	33.8	15.6
Indian ricegrass	0-25	4.7	7.7	33.4	8.8	4.3	5.1	35.0	8.9	4.2	7.7	34.2	8.0
	26-50	4.9	8.5	35.6	9.1	3.9	9.6	35.8	9.4	5.9	9.2	36.7	7.2
	51-75	5.4	8.5	33.3	10.2	4.0	10.3	34.6	6.2	6.8	10.8	32.8	7.8
	76-100	9.8	10.6	38.0	10.4	4.5	11.1	33.9	17.4	9.6	9.2	32.2	8.1
Winterfat	0-25	9.5	9.8	20.6	10.7	8.6	11.1	24.8	9.8	6.9	16.4	21.1	9.3
	26-50	11.0	13.1	19.6	10.0	8.6	12.5	23.4	9.0	9.7	19.8	23.2	8.0
	51-75	10.3	15.2	19.4	10.0	8.6	16.4	23.8	10.6	8.4	22.2	20.8	7.2
	76-100	10.7	15.9	18.7	8.6	9.0	18.5	19.2	12.6	9.9	20.3	18.9	11.8
Four-wing saltbush	0-25	14.3	8.3	11.2	14.9	12.6	9.5	15.0	14.5	11.3	12.3	20.8	12.2
	26-50	13.0	9.9	15.0	13.4	9.9	12.5	25.3	10.2	10.4	12.6	22.0	11.5
	51-75	10.6	12.6	20.2	12.3	9.2	14.2	23.6	10.5	9.4	14.4	25.8	9.0
	76-100	8.4	14.7	31.9	8.3	8.2	19.1	25.6	10.5	7.6	17.5	26.5	6.5

TABLE IV. Analysis of variance for chemical constituents in herbage harvested from eleven dominant desert plants during six dates at four intensities from two locations

		MEAN SQUARES								
Source	D.F.	Ether extract	Total protein	Ash	Lignin	Cellulose	Other carbo.	Phosphorus	Calcium	Gross energy
Species (S)	10	474.46**	269.1**	509.5**	666.4**	3,251.2**	242.76**	.0245**	13.468**	5.450**
Dates (D)	5	17.94**	38.24**	31.64**	58.30**	111.02**	4.57	.0092	.158	.120
S x D	50	3.60	4.00	13.07**	8.26**	19.07	16.15	.0044	.251	.063
Error (a)	66	2.55	3.31	6.88	4.08	24.25	22.73	.0047	.144	.054
Intensity (I)	3	4.07*	3.03**	25.47**	157.00**	17.00	146.00**	.0040	.273*	.095**
I x S	30	4.63**	4.92**	23.61**	9.41**	43.74**	19.76**	.0035	.236**	.060**
I x D	15	2.17	1.07*	4.45**	.90	7.09	4.91	.0050	.122	.028
I x D x S	150	1.66	.70	3.67**	1.29	6.55	9.24*	.0040	.078	.019
Error (b)	198	1.41	.51	1.17	1.43	6.53	6.86	.0042	.086	.017
Total	527									

* Significant at the .01 level.
** Significant at the .05 level.

were considerably higher in ether extract than other browse species.

Ether extract in winterfat, desert molly, four-wing saltbush, yellowbrush, galleta grass, and Indian ricegrass decreased from fall to early spring. For the remaining five species there was no trend (Table I).

In most cases there was no consistent trend in ether extract content as intensity of harvesting increased. Yellowbrush, shadscale, and Indian ricegrass showed a decrease in ether extract with increased intensity of clipping; sand dropseed showed an increase (Table II).

Protein.—The protein content was significantly different among species. The greatest differences were between shrubs and grasses. Shrubs contained more than twice as much protein as the grasses.

Protein content decreased from October 26 to February 24 (Table I). The early-spring clipping, March 31, showed a slight increase in most cases. At the time of this March clipping, buds on some of the shrubs were expanding and showed dark-green color. Indian ricegrass, needle-and-thread grass, and sand dropseed had new growth appearing from the lower sheaths, but galleta grass had none.

The protein content varied widely among clipping intensities for the various species (Table II). From October 26 to March 31 black sagebrush, winterfat, desert molly, yellowbrush, needle-and-thread grass, and Indian ricegrass all showed increased protein content with increased intensity of clipping. Mormon tea, four-wing saltbush, shadscale, galleta grass, and sand dropseed all showed a decrease in protein content with increased intensity of harvesting.

In the first group the plants had more new growth at the bases during March, and therefore the protein content increased with more intensive clipping during this early spring period. However, this does not explain the high protein in the stem bases during fall and winter, which was the case in both shrubs and grasses in this group. This would indicate that many plants retain a high concentration of protein in the bases of the stems, even though they are apparently in a state of dormancy.

Needle-and-thread grass and Indian ricegrass showed higher protein in the bases of the stems, compared to the tips, during the fall and winter. This was understandable, since the bases of the dormant stems, both node and internode, of these two species remained somewhat green and tough most of the winter. This was not true of galleta grass where there was no evidence of green material at any time during the winter. Only slight green coloring was discernible at the bases of the stems of sand dropseed, and this occurred only during a short time in the fall. Thus there is a marked concentration of protein in the bases of some grasses compared to the tips during the winter.

On March 31, all grasses except galleta grass had new shoots emerging from the lowermost sheaths. For this reason, very heavy intensity of clipping gave high protein for the three grasses having new growth available at this time (Table III).

All shrubs except four-wing saltbush and shadscale had materially more protein in the bases than the upper portions of the twigs during early spring. Four-wing saltbush and shadscale had leafy new growth starting near the tips of the previous year's growth and, therefore, had higher protein content in light harvesting compared to heavier intensities during early spring.

Ash.—The ash content in grasses and shrubs was about the same and varied from 4.5% in black sagebrush to as much as 15.1% in shadscale (Table I). The percent in browse tended to decreased as the season advanced; conversely, the percent in grasses increased (Table I).

In general, the ash content of shrubs decreased as the intensity of harvesting increased, and the reverse was true for grasses. Therefore, it appears that the concentration of ash is in the tips of the twigs of shrubs and in the stem bases of grasses.

Lignin.—The percent lignin varied widely among species, but the differences between shrubs and grasses were of greatest importance. Grasses contained only about one-half as much lignin as shrubs (Table I).

The general trend of lignin, with advancement of season, was upward for all species. The greatest increase was during the fall and early winter months.

With the exception of spring, the lignin content in the current year's growth increased with increased intensity of clipping for all species at all times, although this was less pronounced during the fall. This may be the result of a higher stem-to-leaf ratio or a greater concentration of lignified material at the bases of stems, as a result of normal curing process during the fall (Table II).

During the early spring, the heavier intensities of clipping frequently showed a decrease in lignin content (Table III). This was the result of new growth emerging at the bases of the clumps.

Cellulose.—There was a significant difference in cellulose content between grasses and shrubs. Cellulose was approximately 50 percent higher in grasses than shrubs (Table I).

There was a trend toward a general increase as the season advanced from October to March. This was true for all species of both grasses and shrubs.

The effect of intensity of clipping upon cellulose content varied among the various species. The content in winterfat, desert molly, Mormon tea, needle-and-thread grass, galleta grass, and sand dropseed decreased with increased intensity of clipping, but the content in four-wing saltbush and black sagebrush increased (Table II). This was generally true for all harvesting dates.

Other carbohydrates.—Other carbohydrates varied significantly among species of both grasses and shrubs (Table I).

There was a slight tendency for other carbohydrates to decrease from October and November until February, after which there was a small increase.

In Mormon tea and shadscale, these carbohydrates increased slightly as intensity of harvesting increased. In all other species there was a decrease as the intensity of clipping increased.

Gross energy.—The gross energy varied significantly among species, but none was outstandingly high or low. In no case was there any noticeable trend for the gross energy values with respect to advancement of season (Table I).

The gross energy in the harvested material from the different intensities of clipping varied widely among species. In some the energy decreased with intensity of clipping, and in others a substantial increase occurred (Table II).

Gross energy apparently is not influenced to any marked degree by any one of the chemical constituents analyzed, since there were no comparable trends and no paralleling changes with any single component. The high ether extract in black sagebrush and yellowbrush accounts, no doubt, for the high gross energy values of these species. However, the changes in ether extract with season or with intensity of clipping in these species did not show a comparable change in gross energy.

Phosphorus.—The phosphorus content varied significantly among species, and grasses as a group were somewhat lower than shrubs (Table I).

Almost without exception, the phosphorus content of a species changed as protein changed. However, species low in protein did not necessarily have low phosphorus content, and species high in protein did not always have high phosphorus content. In seven species, the phosphorus increased as intensity of clipping increased; and in three species, the phosphorus content decreased with increased intensity of harvesting (Table II).

Calcium.—With the exception of black sagebrush, browse species were considerably higher in calcium than grasses (Table I). There was no apparent trend in calcium as the season advanced.

With increased intensity of clipping, the calcium content in the harvested material increased in galleta grass and decreased in winterfat, four-wing saltbush, and shadscale. In the remaining species there was no trend (Table II).

CONCLUSIONS

Shrubby species were substantially higher than grasses in ether extract, protein, lignin, and phosphorus. Grasses were higher than shrubs in cellulose.

In most cases both grasses and shrubs decreased in ether extract, protein, and other carbohydrates, and increased in lignin and cellulose as the winter grazing season advanced.

Dormant desert plants concentrate the various chemical components in different portions of the past year's growth. For instance, winterfat had a greater concentration of protein and phosphorus in the lower portion of the twig and a higher concentration of ash, cellulose, other carbohydrates, and calcium in the upper portion. Four-wing saltbush differed in that it had a greater concentration of protein and phosphorus in the upper portions of the twigs, and a greater concentration of cellulose in the lower portions. Similar contrasts existed between Indian ricegrass and sand dropseed.

Lignin was the only chemical constituent that was highest in the basal portions of the past year's growth for all species. All other constituents varied widely among species by being concentrated in the lower portions of the stems in some cases and in the stem tips in others.

It was observed that the buds of some shrubs swelled during the fall and winter, whereas in others they awaited warmer weather. At the time of swelling some of the carbohydrates in the stems were, no doubt, converted to protein, since new growth was high in protein. Inasmuch as budding in many shrubs first takes place in the bases of stems, it is believed that a concentration of protein in this portion of the stem is associated with initial budding. At least in some species protein storage in the basal portion of the stem appears to be a normal process.

Protein concentration in the bases of some grasses during the winter dormant period is believed a normal process of curing, but could likewise be a direct result of budding at the lowermost nodes at the bases of the stems. However, late in the winter green internodes were observed above the tiller buds in previous summer's growth. This may explain, in part, the concentration of protein at the bases of the stems of some grasses.

Since phosphorus is closely associated with protein formation, a concentration of phosphorus at the base of the stem would be expected when protein increases.

SUMMARY

A study to determine the chemical content of some important salt-desert forage species and the distribution of the various components in different portions of the plant during dormancy was carried out in west central Utah.

The chemical content in all cases varied significantly among species. Grasses were higher in cellulose; shrubs were higher in ether extract, protein, lignin, phosphorus, and calcium. As the season advanced from October to March, lignin and cellulose showed a general increase; ether extract, other carbohydrates, and protein tended to decrease. The ash content of shrubs tended to decrease as the season advanced, but tended to increase in grasses. There were no noticeable trend for other constituents with respect to season.

Lignin was consistently higher in the basal portions of the stems compared to the stem tips in both grasses and shrubs. In all species but two the content of other carbohydrates was higher in the basal portions of the stem.

In general, the ash content of shrubs was higher in the upper portions of stems, but in grasses ash was higher in the lower portions.

The concentration of ether extract, protein, cellulose, phosphorus, calcium, and gross energy in different portions of the stem varied widely among the species.

It would appear that many plants translocate protein from stem tip to stem base during the winter. Hear greater protection from cold seems to permit maintenance of some green material. Even bud swelling may occur during midwinter in some species. All of these processes tend to make more nutritious forage near the bases of certain species rather than at the stem tips.

References

Aldous, C. M. 1945. A winter study of mule deer in Nevada. Jour. Wildlife Management **9:** 145-151.

Cook, C. Wayne, L. A. Stoddart, and Lorin E. Harris. 1951. Measuring consumption and digestibility of winter range plants by sheep. Jour. Range Management **4:** 335-346.

———. 1953. The effect of grazing intensity upon the nutritive value of range forage. Jour. Range Management **6:** 51-54.

———. 1954. The nutritive value of winter range plants in the Great Basin. Utah Agric. Exp. Sta. Bul. **372.**

Hardison, W. A., W. N. Linkous, and C. Y. Ward. 1957. Digestibility of the top and bottom portions of the alfalfa plant, as estimated from small, randomly collected samples of feces. Jour. Dairy Science **XL:** 768-773.

STUDIES ON THE ECOLOGICAL LIFE HISTORY OF *PORTULACA SMALLII*[1]

David J. Cotter and Robert B. Platt
Department of Biology, Alabama College, Montevallo, Alabama,
and Department of Biology, Emory University, Atlanta 22, Georgia

Introduction

The granite outcrops of the Piedmont Plateau of the southeastern states support a unique flora. For the past two decades their vegetation has been the subject of intensive investigations. One of the endemic plants, which has received little attention, is a small succulent, *Portulaca smallii* P. Wilson (purslane or rock moss).

This study is concerned with the ecological life history of *Portulaca smallii.* The objectives are (1) to investigate the life history of this plant, (2) to study its relationships to the environment, with particular emphasis on environmental extremes, (3) to ascertain its distribution, (4) to investigate its population variability, (5) to attempt to define criteria for its endemism, and (6) to increase our knowledge of the granite outcrop flora.

Most of the plants which inhabit the outcrops represent forms with intrinsic qualities or specialized adaptations which allow them to survive and reproduce under the extreme environmental conditions occurring there. Although many are morphological, these adaptations are primarily physiological or ecological.

The interpretation of the vegetation of the granite outcrops by synecological means is incomplete unless there is some knowledge of the potentialities and limitations of the plants composing the community. Ecological life history studies of the individual plants afford an excellent approach.

P. smallii was chosen as the experimental organism, since it is one of the more numerous of the summer endemics which are subjected to extreme environmental conditions throughout their life cycles. Each particular species presents its own series of problems which can be investigated ecologically, but the use of an endemic species which grows in great numbers in neighboring localities allows more intensive study. The study of endemic species also involves a simpler set of environmental variables than ones which grow over a wider range.

Literature Review

Several of the granite outcrop plants which have been the subject of individual investigations are *Diamorpha cymosa* (Nutt.) Britton (McCranie, 1938; Wiggs, 1956); *Isoetes melanospora* Engelm. (Johnson, 1938); *Amphianthus pusillus* Torr. (Lunsford, 1939); *Sabulina brevifolia* (Nutt.) Small (Stipe, 1939); *Gelsemium sempervirens* (L.) Ait. F. (Speer, 1942); *Talinum teretifolium* Pursh. (Guptill, 1947); and *Grimmia laevigatum*

---

[1] This study was supported in part by a research contract No. A T-(40-1) 2089 from the U. S. Atomic Energy Commission.

(Brid.) Brid. (Keever, 1957). Although the major emphasis of most of these studies was morphological and cytological, the ones by Wiggs and Keever were primarily ecological and made significant contributions to the understanding of the problems of these outcrop plants.

The flora of the granite outcrops has been studied widely. Smith (1938) and Matthews (1941) gave descriptions of the local floras of Stone Mountain and Mount Panola respectively. Baker (1945, 1956) described the floristics and the seasonal aspects of the plants on the outcrops near Atlanta, Georgia. An account of the vegetation of the major outcrops of the Piedmont was given by McVaugh (1943). This work focused attention on the most characteristic species. Burbanck and Platt (unpublished data) have completed an exhaustive study on the analysis of the vegetation of Rock Chapel Mountain, Rollaway Mountain, and Mount Arabia.

The succession patterns of the vegetation have been the subject of two investigations by Oosting and Anderson (1937, 1939) and another study by Keever, Oosting, and Anderson (1951). These studies in North Carolina have led to the establishment of the paths of xeric succession on granite outcrops. McVaugh (1943) devoted a short section of his paper to succession, and Whitehouse (1933) described the successional patterns on a granite exposure in central Texas. Platt and Witherspoon (1959) have studied the ecological effects of x-radiation on the structure of granite outcrops communities.

Description of the Area

Outcropings of exposed granite occur within a broad band about 100 miles wide in the Piedmont section of the southeastern United States. The size of the exposed rock varies from small exposed boulders to large outcrops over several hundred acres in extent. They form a chain of semi-isolated islands of granite through the Piedmont from southern Virginia to eastern Alabama.

The largest concentration of granite outcrops is near Atlanta, Georgia. Within a 25-mile sector east and south of Atlanta are found 6 major outcrops; Stone Mountain, Mount Arabia, Rollaway Mountain, Pine Mountain (Little Stone Mountain), Rock Chapel Mountain, and Mount Panola. The composite acreage of these 6 residual monadnocks totals over 2,000 acres. Interspersed between these larger outcrops are many smaller flat rocks, often called basement or pavement rocks, ranging in size from a few square feet to over 100 acres.

Each of these outcrops may be different from the geological viewpoint. For example, in the Atlanta area the outcrops are divided into two categories, the Stone Mountain granite type and the Lithonia type, which is a contorted granitic gneiss. The rocks vary in color, grain, hardness, age, mineral composition, and many other characteristics. Watson (1902) and Herrman (1954) have given adequate geological descriptions of this area. Granite, gneiss, and schist are igneous rocks which underlie much of the Piedmont section and form the parent material for the soils of this region.

There are over 275 different plant species from the granite outcrops in the collection at the Emory University herbarium. These plants may be divided into 4 groups on the basis of their appearance on the granite outcrops. About 15 endemic species, including *P. smallii,* grow exclusively on granite. Another group of about 30 plants find the conditions of the habitat optimum for good growth and have become part of the typical flora. Many of these species have a discontinuous distribution, occurring on the granite outcrops in the Piedmont and inhabiting other areas such as sandstone outcrops elsewhere. There is a group of approximately 50 weedy plants which invade the outcrops and find conditions suitable for growth. Many of these plants are usually considered to be characteristic of the surrounding woods and open fields. In addition to these characteristic plants which compose the major element of the vegetation, there are over 150 species which are occasionally found on the outcrops.

The 6 distinct habitat regions on the outcrops are: the bare rock, crevices in the rock, rock rubble, weather pools, vegetation mats, and the ecotone between the exposed granite and the

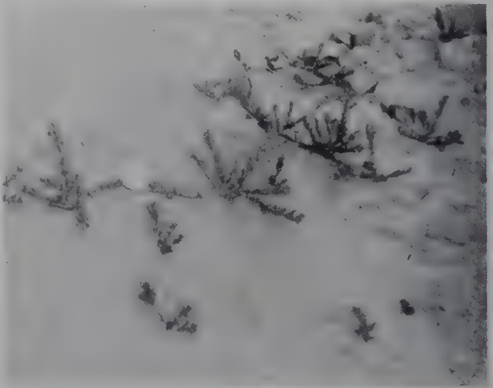


FIG. 1. *P. smallii* in the natural habitat showing growth form.

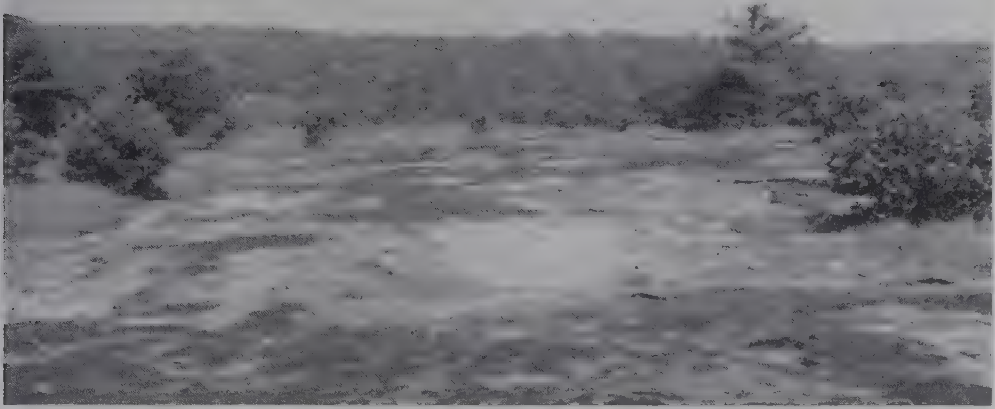


FIG. 2. An *aspect* view of Mount Rollaway showing numerous extensions of soil on the bare granite. The ecotone between the bare rock and the accumulated soil is the typical habitat for *P. smallii.*

surrounding vegetation. *P. smallii* is the dominant plant in the narrow outer band of shallow soil in the ecotone between the exposed granite and the marginal vegetation.

Several factors are limiting throughout the year and prevent any drastic change in the vegetation of the outcrops. The major factors are erosion, which limits the accumulation of soil, the shallow soil, extreme temperatures, drought and inundation, high insolation, winds, fires, and pH. Conditions are such that only a few plants with suitable ecological tolerances are able to survive.

The Plant

Portulaca smallii is a succulent summer annual (Figures 1 & 2). According to the original description by Wilson (1932), it is a spreading herb up to 15-18 cm high with linear-terete, alternate leaves, 1.2 to 1.5 mm wide and 1.0 to 1.5 cm long, and inconspicuous axillary hairs. The perfect terminal flowers, surrounded by an involucre of 10 or more leaves, have 4 or 5 "pinkish" petals. The oblong-elliptic to elliptic-ovate or ovate petals are 3 mm long and 1.5 mm broad, and the deltoid-orbicular sepals are 3 mm long and 3.0 to 3.5 mm wide.

There are 8-12 stamens. The stigma has 4 lobes. The inferior ovary contains many ovules attached to a basal placenta. The fruit is a subglobose capsule, circumscissile a little below the middle. The seeds are reniform with a minutely tuberculate black testa when ripe. The range is the granite outcrops of the Piedmont of the southeastern states (Small, 1933). The type locality is Little Stone Mountain, DeKalb County, Georgia (Wilson, 1932).

In his monograph Wilson split off *P. smallii* from *P. pilosa* L., its nearest relative, on the basis of its range, number of stamens, the amount of hairiness, and other characters which differed only slightly in a quantitative way. *P. pilosa* is found in the Coastal Plain and the adjacent provinces, while *P. smallii* is restricted to granite outcrops. *P. pilosa* has from 15 to 32 stamens and *P. smallii* from 8 to 12. *P. pilosa* has slightly more hairs (light brown in color) than its counterpart on the granites. McVaugh (1943), as well as others, has supported this division, stating that there appear to be enough differences in these two plants to warrant separate species. Thus all plants which fit the latter description and are found on granite are identified as *P. smallii.* Confusion arises with respect to specimens collected prior to 1932, and possibly to some others, due to the omission of *P. smallii* from some of the keys to the flora of the southeast.

Several other members of this family occurring on granite are *Talinum teretifolium, Talinum mengessii* W. Wolf, *Portulaca oleraceae* L., and *Portulaca coronata* Small.

This paper is based in part on a dissertation submitted by the first-named author to Emory University in partial fulfillment of the requirements for a Ph.D. degree.

MATERIALS AND METHODS

This study of the life history of *P. smallii* is based on data obtained from observations and experiments in the field and laboratory. The field work extended from September, 1955, to September, 1958. It consisted of direct observations of the plant in its natural habitat with the purpose of determining environmental relationships, characteristics of growth and development, and distribution. To this end, weekly trips were made to the outcrops during the growing seasons of 1956 and 1957. Mount Arabia, a large dome-shaped outcrop 20 miles southeast of Atlanta, was chosen as the major experimental area because of the presence of a large population of *P. smallii*, its accessibility and relative freedom from disturbances, and because this area has been studied extensively in the past.

In addition to the weekly trips to Mount Arabia, more than 100 trips over the three year period were made to other local outcrops to examine conditions occurring elsewhere. Furthermore, ten trips were made through Georgia and Alabama to locate stations of *P. smallii* and to analyze the character of the populations of plants which grew in these localities. Although the outcrops visited varied in many ways, they are essentially similar with respect to the conditions in which *P. smallii* grows. Mount Arabia is typical of the outcrops which support *P. smallii*, and the data obtained on this outcrop are indicative of the type of results to be expected on other outcrops throughout its range.

The laboratory aspect of the problem was designed to supplement field observations and to investigate the responses of the plant to individual phases of the environment under controlled conditions. Efforts were made as far as possible to maintain a single factor variation during each of the experiments. These studies were conducted in the greenhouse of Emory University. The soil and experimental material were collected from Mount Arabia.

Temperatures were recorded by Six's type maximum-minimum thermometers. Crude rain gauges, consisting of a bottle, funnel, and a layer of mineral oil, were used to measure precipitation. Light intensity was determined by a Model 200, Photovolt Corporation photometer. Cup adaptors were used to read high light intensities and the readings converted. An American Instrument Company Model 4-96 circulating constant temperature bath was used for the determination of the temperature tolerances of the plant. Specific methods used in the different laboratory experiments are briefly discussed in the following section when necessary for the clear presentation of the experimental data.

OBSERVATIONS AND DISCUSSION

Field Work

Distribution.—On the basis of the trips made throughout its range, the strict endemism of *P. smallii* to the granite outcrops of the southeastern Piedmont from North Carolina to Georgia has been reaffirmed. The occurrence of these plants was found to be sporadic, with great variations occurring in population density. For example, some of the small outcrops near Atlanta do not support it, and on some of the larger outcrops it does not grow in habitats which seem to be suitable. Near Sparta, Georgia, there is another typical illustration of fortuitous distribution. Two outcrops of three acres in extent are separated by a road. Although identical in most respects, one supports about 2,000-3,000 plants while the other has less than 300.

Curiously, the plant was not found on the outcrops in South Carolina, and no records have been located as to its occurrence there. Also, no reports have been located of its occurrence in Alabama or on other types of outcrops such as sandstone or limestone. There were only three instances observed where *P. smallii* grew on substrate other than granite—once as a weed in the front yard of a residence where the dry bermuda grass of the lawn rendered only token competitition in only a few portions of the dense growth of *P. smallii*, and in two first-year abandoned fields with only a minimum of competition afforded by the sparse pioneer invaders. In each case the exposed granite was less than 20 meters away.

Although there are no specific adaptations of this plant to favor seed dispersal, three explanations may be presented for its present distributional pattern. Harper (1939) suggests that the violent wind storms such as hurricanes and tornadoes function in the dissemination of seeds from outcrop to outcrop. It is possible that birds aid in dispersing the seeds. Martin *et al.* (1951) indicate that seeds of a related plant, *P. oleraceae* L., are eaten by birds. It may be that the populations occurring on the outcrops today are relics of a past wide-ranging species, or a newer derivative of the closely related Coastal Plain species, *P. pilosa.*

From observations it appears that *P. smallii* represents a stable population with little shift in area and seems to be a strict endemic of the granite outcrops of the Piedmont of the Southeastern states.

The Habitat.—The general characteristics of the habitat of *P. smallii* have been given above. More specifically, it has been found usually on the periphery of the granite outcrops in a sharply marked ecotone between the exposed rock and the surrounding vegetation. This narrow band is characterized by shallow soil and paucity of vegetation. The width of the area is dependent upon the slope of the surrounding rock which governs the severity of erosion. If the ecotone is not present, it is usually replaced by a buffer zone of mosses. *P. smallii* is also frequently found in the debris from past quarrying operations, but seldom found in the other habitat areas of the outcrop.

The distribution of *P. smallii* on an individual outcrop is related to the conditions of habitat which determine its establishment. There must be an adequate supply of water following germination to insure establishment. The area on the edge of the outcrop is ideal, since it receives and retains water from runoff. The other factors important in the distribution of the plants on an outcrop, high light intensity and relative freedom from competition, are satisfied in the marginal ecotone. Frequently plants are found growing in the isolated islands of soil of small depressions where similar teleological conditions obtain. Severe water erosion precludes the establishment of the plants on steep slopes.

The populations on the outcrops appear to be relatively stable and no significant changes in density were observed during this study. *P. smallii* does not seem to be expanding, since it does not occupy all the available niches on the outcrop which seem to be favorable for optimum growth. It is only in the rock rubble from past quarrying operations that any indication of the aggressive invasion of the plant can be witnessed.

The Physical Environment.—The average yearly precipitation for the Atlanta area is about 130 cm and is fairly evenly distributed through the year. Occasional prolonged dry periods may last for several weeks. The winters are not very severe and the temperature seldom falls below —6° C. Daily temperatures in the summer rarely exceed 38° C.

Table I presents the data from some of the environmental measurements obtained over a seven-week period during the summer of 1956 on Mount Arabia. The weekly maximum and minimum temperatures were recorded from the exposed areas and from the surrounding woods. Since it was necessary to hide the thermometer on the outcrop under a pile of rocks to prevent vandalism, the temperatures are not as high as those occurring at the rock surface.

Precipitation as determined by rain gauges is expressed in mm per week. The soil samples, representing wet, intermediate and dry situations, were taken weekly from a large soil-covered depression and analyzed for soil moisture. The majority of the habitat areas for *P. smallii* were between the intermediate and the dry conditions. However, *P. smallii* does grow in both wet and dry extremes of the experimental area, which represent the extremes in soil moisture found on the outcrops.

TABLE I. Environmental data

	7/16	7/23	7/30	8/6	8/22	8/30
Maximum temperature (C°)						
a. woods	41	34	38	37	39	37
b. outcrop	46	39	44	45	47	40
Minimum temperature (C°)						
a. woods	16	20	19	20	19	17
b. outcrop	12	18	18	20	19	14
Precipitation (mm) (outcrop)	68	5	25	19	19	
Soil moisture (outcrop)						
a. wet		31.7%	32.6%	22.2%	32.3%	
b. intermediate		6.9%	15.2%	7.9%	6.3%	
c. dry		0.4%	0.7%	0.2%	3.5%	

The contrast between these two habitats would be much greater had it been possible to measure the temperatures on the granite unhampered by the protective cover of the rock rubble. It is expected that temperatures in the seedling microenvironment surpass 70° C., due to high insolation and the absorption of heat by the dark soil and the granite surface. The extremes in soil moisture, ranging from air dry to saturated, present a typical picture of the summer conditions on the outcrops. The sandy nature of the soil accentuates these extremes. Strong winds and high temperature combine to parch the soil and sear plant life, and only in areas where runoff water from rain is able to accumulate or in areas with deep soil is there sufficient moisture to maintain plant life.

The Biotic Environment.—Three insects feed on the plants in the field: a larval leaf beetle, a red spider mite, and a spring-tail. The larvae of the leaf beetle were collected, allowed to pupate under a screened chimney lamp, and identified as *Disonycha* sp. These larvae feed on the leaf tips, leaving a typical wound observed on many of the plants in the field. The adult spring-tails, *Collembola* sp., feed in the same area of the leaf, possibly on the open wounds left by *Disonycha*. In the laboratory the plants were attacked by the majority of the common green-house pests. Three different species of Hymenoptera were observed visiting flowers and seem to be agents for cross pollination. Capsules with small circular borings, of undetermined cause, containing partially eaten seeds were frequently observed in the field.

P. smallii was found growing with many plants, but *Talinum teretifolium* Pursh., *Cyperus granitophilus* McVaugh, and *Stenophyllus capillaris* (L.) Britton occurred consistently enough in the narrow peripheral soil band to be considered as associates with *P. smallii*. It is interesting to note that when *P. coronata* Small occurred on an outcrop, it was in an area near *P. smallii*. The number of plants which grew in association with *P. smallii* increased in the rock rubble habitat.

P. smallii does not grow as densely as many other outcrop species, the maximum observed being 188 per square decimeter. Density of plants seemed to be predicated on the conditions of habitat, seed supply, and the ability to become established. They were never found under a heavy overstory of herbaceous plants when they occasionally invaded the marginal vegetation.

Soil.—Soil was collected from the outcrop and brought into the laboratory for textural analysis. The methods used are described by Bouyoucous (1937) and Kilmer and Alexander (1949) under the mechanical separation of sands by the rapid hydrometer method. The separation of sands was also conducted by using a nested series of sieves. Duplicate series from areas 6 feet apart were run, using both of these techniques, and gave the range of 82% to 83% sand. Mechanical analysis of the soil revealed that there was 12% silt present; 5% was clay. The combination is a loamy sand (Lyon, Buckman and Brady, 1952). A breakdown of the results of the separation of the sands shows that 38.7% is fine gravel, 15.6% coarse sand, 12% medium sand, 21.7% fine sand, and 12% very fine sand. Measurements of the soil at other places on the outcrop are expected to vary slightly from this pattern, but the soil is mostly of a sandy nature.

Transplant Quadrats.—Transplant quadrats were attempted during the 1956 and 1957 growing seasons. Plants were lifted out of their natural habitat in the ecotone in square decimeter blocks of soil which extended down to the granite surface. In this way few of the plants were disturbed. These intact soil blocks were moved to areas of the outcrop which did not support *P. smallii*: a runoff area, in the surrounding woods, in the marginal vegetation, and three weather pools: a mature community, a moist solution pit, and a barren dry one. They were then placed in the soil and the soil watered to saturation. Periodic observations were made on the conditions of the plants.

The transplants in 1956 were unsuccessful; all but one of the 300 plants perished within three weeks. In 1957 rain followed the transplanting and plants became established and grew to maturity in the run-off area, the dry solution pit, and the mature community. In the moist community the plants were killed by inundation and they failed to become established in either the marginal vegetation or the woods.

Phenology.—*P. smallii* seedlings were first observed on Mount Arabia on July 7, 1956, and June 24, 1957; flowers were first observed on July 30, 1956, and July 16, 1957; and fruits were seen a week after flowers. The majority of the plants were dead by October 26 in 1956 and November 20 in 1957. Within this population germination occurred over a three-week period and floral production started about one month after germination and continued until the death of the plants. Germination, establishment, flowering and death may vary widely among members of a population. A small group of about 30 plants was observed in a small moist depression on June 7, 1958. There were no other *Portulaca* on the outcrop at this time, although large populations had been present the previous two years. The only difference in the area in which the plants were found and the rest of the outcrop was the persistence of the water in the soil.

The timing of each critical phase of the life cycle varies from year to year. An Emory University herbarium sheet dated July 1, 1939, contained a plant with mature fruits, indicating that germination occurred early in June. According to Wilson (1932), Small collected a specimen of *P. smallii* in January of 1894 on Stone Mountain, indicating that this year the plants persisted for a long time.

Fourteen permanent quadrats were established in 1956 in a number of habitats in which *Portulaca* was growing. These quadrats were used to supplement field observations on phenology. Measurements of relative growth and survival in each of these quadrats show that in the dry areas growth was inhibited, flowering delayed, and higher mortality rates prevailed. The major cause of death is desiccation. Insect damage, inundation, and uprooting from heavy rainfall also kill many plants.

The height of floral activity occurs about two months after germination and is followed by a senescent period of declining vigor and a reduction in the tolerances and the physiological activities of the plant. The accompanying loss of physiological adaptiveness of the plant in the senescent period makes it hard to ascertain the exact causes of death. The length of time that plants remain alive in the field is variable from year to year, but the occurrence of hard freezes in the late fall probably terminates the life cycle. The dead plants sometimes persist through the following spring, occasionally, with seeds retained in the capsules.

The permanent quadrats in the field revealed that there is much variation in the timing of the processes within a population. The phenology of the plant is controlled by the date of germination, which varies from year to year and may extend over a period of three weeks. The microenvironment of the seedling as well as the genetic differences in each plant dictate the timing of the processes of the individual plants in the population. The most critical phase regulating the pheonology is the date of germination. In *P. smallii* germination is dependent upon two major factors, high temperatures and rain. Since the climate varies from year to year, the date when optimum temperatures and adequate moisture coincide would be expected to vary. Likewise, establishment, amount of growth, flowering, seed production, and death vary within the population as a whole and are dependent to a large extent upon the climate for a given year.

From the above discussion, it is evident that it is impossible to define precisely the growth and pheonology of the plants from year to year. It may be stated generally that germination occurs about the first of July, the first flowering about one month later, fruits and ripe seeds the following week, the height of floral activity in late August, followed by a senescent period of varying length which is terminated by hard freezes in the late fall.

Population Variability.—Early in the course of the field work it became apparent that there was a wide range of variation in the morphology of *P. smallii* which is not included in the description of the species. Particularly the floral structure differs markedly, even among flowers of the same plant.

The growth habit may be erect, ascending, or procumbent. Size of mature plants varies from 1-30 cm. The leaves are 7.3 to 18.3 mm long and 1.2 to 2.0 mm wide. There are frequently less than 10 involucre leaves, and even as few as four.

Although the number of stamens is described as 8 to 12, as many as 25 and as few as 4 have been observed (Fig. 3). Quite often some of the stamens may be abortive. The number of stylar lobes is set at 4, yet flowers with 2 to 7 lobes have been observed. Three flowers were noted which had only three petals. Petals may be notched one or two times, and the color of the corolla may vary from a deep lavender to a lightly colored tip to a pure white. The color of the petals seems to be the same for all flowers of the same plant. The filament may be red if the petals are deeply pigmented, but the common color is white. The passage of the flower over the fumes of a strong acid or base does not affect the color of its parts.

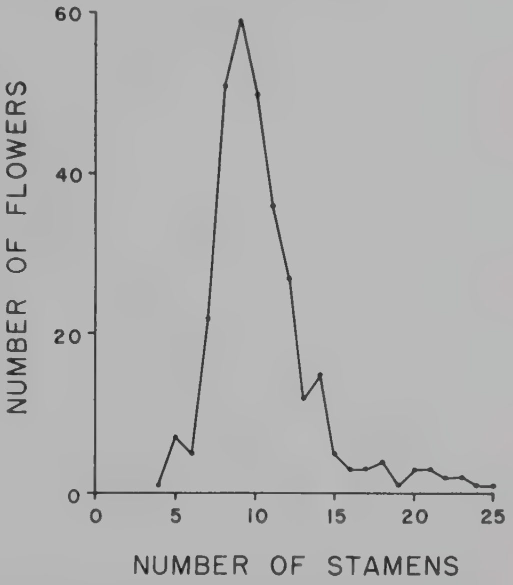


FIG. 3. The frequency of the number of stamens of *P. smallii* flowers in 12 outcrop populations and the greenhouse. Thirty-seven per cent of the observations were outside the limits of the description of *P. smallii* by Wilson.

Intensive studies on Mount Arabia were made to determine the extent of variation within a population. The following measurements were taken: number of involucre leaves, number of stamens, number of stylar lobes, number of petals, color of petals, width of petals, length of petals, width of sepals, length of sepals, width of leaves, length of leaves, amount of hairiness, pigmentation of leaves, growth habit, and number of primary branches. Plants for these and subsequent measurements were selected at random. There were no correlations between these factors on the basis of scatter diagrams, and genetic control had wide amplitude, since these factors varied on the same plant.

Since the differences between *P. smallii* and *P. pilosa* are largely quantitative, a series of measurements was taken from several populations to ascertain if there were gradients of resemblance of these species in different populations. Plants from 12 outcrops were studied. Of those investigated, one of the populations at Mount Arabia approximates most closely the description of *P. smallii.* The Sparta, Georgia, population represents the southernmost area investigated, and is closest to the range of *P. pilosa.* The population of Little Stone Mountain, the type locality, shows a degree of divergence. The plants from North Carolina are the smallest and have the fewest stamens and stylar lobes of those populations examined. There were no evident trends indicated from the measurements of the number of involucre leaves, color of flowers, number of petals, plant size, or leaf size.

The relationship of the number of stamens and number of stylar lobes is presented in a group of scatter diagrams of five selected populations (Fig. 4). There were no geographic trends established in the course of the investigations.

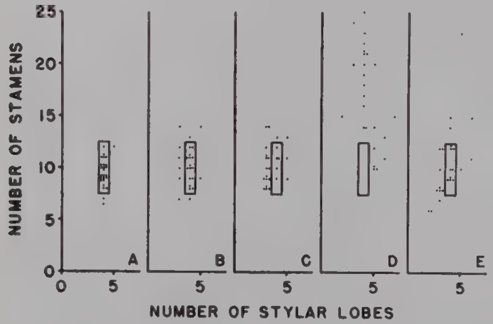


Fig. 4. Variation in number of stamens and stylar lobes exhibited by populations of *P. smallii* at (a) Mount Arabia, (b) Mount Arabia, (c) Sparta, Georgia, (d) Mount Rollaway, and (e) the type locality, Little Stone Mountain. The area encompassed by the solid lines includes the limits of *P. smallii* as described by Wilson.

The occurrence of wide variations in the structure of *P. smallii* beyond the limits described indicates the inadequate and perhaps inaccurate description of the plant in the literature. Often within the same population and even on the same plant there are some flowers which fit the ascribed limits of *P. smallii* and others which fit the description of *P. pilosa.* Analysis of the data on the number of flower parts indicates that all of the members examined belong to the population of *P. smallii.* The overlap in the characteristics toward *P. pilosa* can be expected to occur at rather low frequencies.

The vegetative characteristics of the two species are quite similar and only the slight increase in size and amount of hairiness can be detected in the comparison of the two. The similarity of the plants is further strengthened by the fact that there are 16 chromosomes for each species (Steiner, 1944). The differences between them are quantitative rather than qualitative. The major criterion for distinguishing these plants appears to be whether they occur on granite. On the basis of the observations made, the taxonomic status of *P. smallii* appears to be justified, but further study is necessary before a firm conclusion can be reached. The exact relationship between these two plants and the validity of assigning a species rank to *P. smallii* could only be determined by detailed cytological investigation of both plants and breeding experiments.

Some confusion may be engendered by the splitting of the species, and the identity of specimens before 1932 may be in question. Even at the present time there may be some doubt about the identity of specimens since *P. smallii* is not covered in some of the analytical keys in use. Whitehouse's reference to the occurrence of *P. pilosa* on the central Texas granite may actually be *P. smallii.* These questions are important to the understanding of the distribution of the species.

Laboratory Investigations

Germination.—Since early germination attempts failed, it was postulated that the seed coat was impervious to water. Untreated seeds soaked in water overnight failed to gain weight, thus demonstrating that the testa prevented the penetration of water. Seeds with ruptured seed coats imbibed water and germinated. There was no after-ripening period necessary for mature seeds; and by mechanically removing the testa, seedlings were available at any time.

Despite several periodic attempts in the winter of 1955, the first successful germination of untreated seeds was not until May 26, 1956. Throughout the summer of 1956 untreated seeds germinated under many different light and temperature conditions, but in 1957 germination of untreated seeds could be obtained only in full light in the greenhouse. The reasons for this are not understood.

On April 26, 1956, one week after soil from Mount Arabia was brought into the greenhouse and watered, *Portulaca* seedlings appeared. Germination in the greenhouse occurred in April, 1956; late March, 1957; and early February, 1958. These dates are much earlier than the corresponding germination dates in the natural habitat. The high temperatures in late June and early July, coupled with moist conditions, trigger the germination of the plant in nature. The earlier germination in the greenhouse can be attributed to the earlier occurrence of these two factors.

Only 32 of over 1600 seeds germinated in a constant temperature room over a two-month period. These seeds represented an experiment on the effect of density of seeds on percentage germination. Seven months later, after a short exposure in the greenhouse, germination percentages from 30% to 70% were attained. There was no effect on germination with density of seeds from 50 to 350 per petri dish. The differences in the percentage of germination are due to a change in the permeability of the testa, since it has been previously demonstrated that an after-ripening period of the embryo is not required. The highest germination percentage recorded was 96% and the average was about 70%.

Seeds representing 1939, 1940, 1946, and 1947 were taken from pressed herbarium specimens to investigate the viability of *P. smallii* seeds. The testa was removed from half of the seeds, while the other half were left intact. None of these seeds germinated after a year's exposure to moisture and greenhouse conditions. Factors of storage, particularly the presence of cyanide in the herbarium cabinets, may have destroyed the viability of these seeds. Seeds collected in 1955 and stored at room temperatures remained viable for 2.5 years. The maximum period of viability is expected to surpass 2.5 but the actual length of time could not be established.

Growth and Establishment.—The first sign of germination is the emergence of the radicle and is rapidly followed by the elongation of the hypocotyl and the appearance of the two cotyledons. The seed coat may adhere to one of the cotyledons for a short time, but in no instance has the binding of the cotyledons by the seed coat hindered complete germination. The cotyledons are functional and persist unless environmental stresses cause their abscission.

The new leaves are produced within a whorl of upturned previously-formed leaves, which give the impression of an involucre. There are usually three young leaves of different lengths inside the whorl, which became part of it when they approach maturity. As stem elongation and growth continue, leaves are given off on alternating sides of the stem. Mature plants have a three-eighths phyllotaxy.

Flowers originate later within this same area. The floral primordia may be distinguished from the leaf primordia by their red color and their shape. Flowers are terminal except for occasional axillary ones. There is a broadening of the floral head with the continued production of flowers. Increases in the number of leaves which comprise the involucral bracts occur along the margins of the involucre in an indefinite pattern, and occasionally one will be found in the middle of old flowering heads.

The formation of branches is similar to the growth process in the main stem except in its early stages. The first sign of a new branch is the appearance of small leaves in the axis of the cauline leaves. The beginning of the elongation of the branch can be seen as the number of leaves increases.

Branching occurs from the base upward in the axis of the lower leaves. After flowering has been initiated branching may then occur in the area immediately below the flower, so that some of these branches may surpass the height of the main stem. There may be a gap at the middle formed at this time with the higher branches being formed, perhaps indicating a change in the auxin relationships. Branches may also give off a number of secondary branches.

The first indications of the growth form appear early and seem to be contingent upon both the timing and vigor of the early branches. Thus the control of the pattern of growth is either dependent on apical dominance or may lie in a modification of this dominance. If the plant is prostrate or ascending, the main stem will bend a few centimeters above the soil surface and the number and proximity of the side branches will increase markedly in comparison to an erect plant.

Establishment is the most critical phase of the life cycle. Decrease in survival in the drier permanent quadrats indicates that water is essential for good establishment and greatly determines the growth and vigor of the mature plants. The transplant quadrats illustrate that *P. smallii* can become established and grow in areas of an outcrop which do not generally support it only if there is an adequate water supply during establishment. A prolonged inundation during the critical establishment phase is detrimental to good growth, and if the water entirely covers the young seedlings they will die.

The establishment and growth of *P. smallii* is largely controlled by water supply, but other environmental factors also regulate these processes. Relative humidity indirectly effects the growth of the plants by its influence on evapo-transpiration rates affecting the amount of moisture available to the plants. After the plants become established they are able to withstand wide fluctuations of moisture.

Reproduction.—Members of the Hymenoptera and possibly other insects pollinate flowers in the field, but greenhouse flowers are mostly self-pollinated. The flowers of the plants placed in low light intensities fail to open. These unopened flowers, as well as flowers from isolated plants, produce fruits and seeds, thus proving that the flowers are truly self fertile. Isolated emasculated flowers failed to produce seeds. Flowers are open only a short time around noon and the flowers that are not cross pollinated may be later self pollinated as the petals and stamens fold inward following flowering. The reproductive potential of the plant varies, but the number of flowers is dependent on the size and vigor of the plant.

Flowers marked with indelible ink were opened periodically to determine how long it takes for the seeds to ripen. In seven days the seeds began to take on a brown color and by the eighth day the seeds had fully developed seed coats and were similar in appearance to other seeds. These seeds germinated if the testa was ruptured with a dissecting needle.

The number of seeds per capsule is variable, but in general the larger plants had the highest yield per capsule. Figure 5 shows the frequency of number of seeds per capsule. Drought-stunted plants in the field average one or 2 capsules per plant and only 2-4 seeds per capsule. Several capsules were empty. Often in capsules with 4 or 5 seeds, the seeds were visibly larger than others from the same plant. The plants grown from these seeds are much larger, as shown in Figure 6. The dead corolla fuses to form a calyptra-like cap over the top of the capsule and may persist until the capsule opens. Capsules may open two to four weeks after formation but there is no specific mechanical adaptation to free the seeds from the lower shallow cup-like portion of the capsule, which usually remains attached to the plant. Often the numerous hairs inside the involucre delay the release of the seeds.

In the greenhouse some of the leaves which fall off the plants develop adventitious roots and become established in the moist soil. Roots as long as six cm developed from these leaves, but there was no aerial growth and the leaves remained alive for as long as two months. Occasionally there was a slight swelling of the root just below the leaf. Excised stems develop adventitious roots and become established if the soil is kept moist. Within one week 25 plant cuttings developed roots systems with some roots as long as 3.5 cm. Although it reproduces well from cuttings, this is not a factor in the natural habitat.

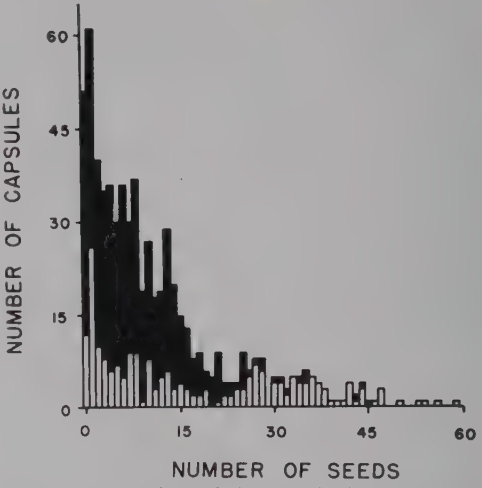


Fig. 5. Comparison of the reproductive potential of different size plants; the black bars represent the total number of capsules and seeds of 25 plants selected at random, while white represents these for a single large plant. The 443 capsules of the small plants contained 3,751 seeds for an average of 8.4 seeds per capsule, while the 214 capsules of the large plant contained 3,662 seeds for an average of 17.1 seeds per capsule. This reproductive differential could be increased tenfold by the selection of the plants.

The ability of the plant to root from excised portions gave rise to an experiment in which branches from large plants were placed in several soil conditions to determine environmental influences on floral morphology and the variations encountered. Cuttings from 5 plants were placed in A_2 and B_2 horizons of a Cecil soil, the disturbed A and B horizons of a Madison soil, in cinders, gravel, sand, granite soil fertilized with a commercial fertilizer, shallow granite soil, and in the B_2 of a soil derived from granite, probably a Durham or Appling soil. Care was taken to omit from consideration the floral primordia which had already begun development on the cuttings, so that influences of the previous conditions would be held to a minimum. Observations showed that there were variations in the floral structure between cuttings growing in the same soil, variations between cuttings of the same plant, and even variations on the same cutting. The cuttings in the fertilized granite soil showed the most vigorous growth, but all cuttings became established in each of the soils tested. This experiment demonstrates that floral variability is controlled by innate genetic properties of the plant and that

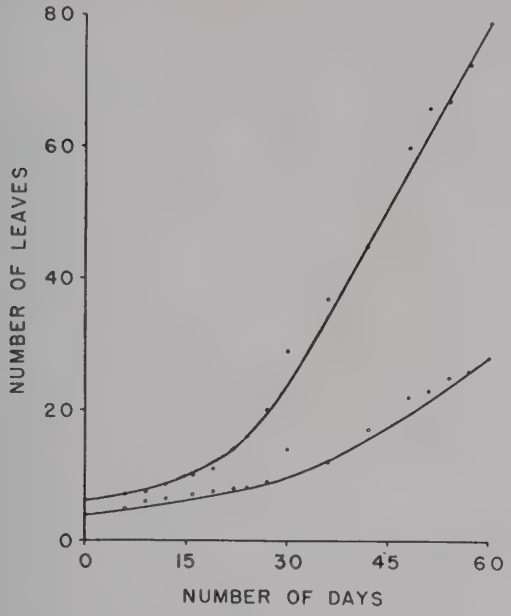


FIG. 6. Comparative growth of plants from large and small seeds. Dark circles indicate the average number of leaves for 10 plants grown from larger seeds; the open circles indicate plants grown from 15 smaller seeds. Measurements were taken approximately every three days.

the soil does not influence morphological expression in the flower. Other observations of the plant in the greenhouse and the field showed floral variability, but no environmental cause was indicated.

The genetic control of floral morphology is evident since flowers on the same plant, cuttings of plants placed in different environmental conditions, and observations of flowers revealed an indefinite non-pattern variation and failed to demonstrate any environmental modification of the floral characteristics of the plant. The control of the variation probably lies in the genetic expression during floral development. Most of the vegetative and physiological characteristics of the plant can be modified by changing the environment.

The Drought Response.—The drought response is similar, whether it is found in the field or in the laboratory. After a prolonged dry period the succulent leaves bend upward toward the stem and begin to wrinkle with the loss of water. When the drought is severe, all water is lost from the leaf and it shrivels, turns brown, dies, and falls off the stem. The drought symptoms progress up the main stem, affecting the lower leaves first, then leaves higher on the main axis and the branches toward the tip. Those leaves which are on the main stem at the base of the branches are the most easily injured. The involucre leaves persist the longest time, even after the stem dies.

In a very severe drought the stem turns brown and withers, with death of that portion of the plant which it supports following irrevocably. If the drought is moderate, the leaves in the first stage of withering will regain their turgor and survive. New small leaves will often arise in the axis of the old fallen leaves and begin to form a new branch. Drought provokes more serious injury to older plants than to young plants, which are able to survive long drought periods without showing any strong reaction to the drought conditions other than the cessation of growth.

Desiccation.—Ten similar pairs of plants selected from green house flats were divided into matching groups. The stems of these plants were cut at the soil line and sealed with vaseline. The first group of ten plants was suspended on a grid of hardware cloth over water in three sealed desiccators. The second group was placed in similar desiccators which were filled with silica gel and calcium chloride to preserve a low humidity. All the desiccators were stored in a room which maintained temperatures from 20° to 22° C. and had indirect lighting from windows.

Observations on the number of leaves and the status of the reproductive organs were made every two days. The results, based on the number of surviving leaves, are shown in Figure 7. In the dry experimental group the response to the treatment was the typical drought response. In contrast, the leaf drop from the wet group was characterized by a yellowing of the affected leaves, which fell from the plant in a turgid state. The succession of leaf drop was the same for both groups; that is, leaf drop progressed up the stem. Leaf drop was moderate the first ten days in both groups. During the next six days leaf drop in the dry group amounted to about 65% of the total number of leaves, while the wet group dropped less than 10% of their leaves. By the end of the third week of treatment, all of the plants in the dry group were dead, whereas it took thirteen weeks for all ten of the plants in the wet group to die.

Flower production and ripening of the fruit continued after the treatment started. The ten "dry" plants had nineteen floral units at the initiation of the experiment and had forty-three before it was terminated by the death of the plants; the "wet" plants, in contrast, had eleven floral units at the start and twenty-eight by the third

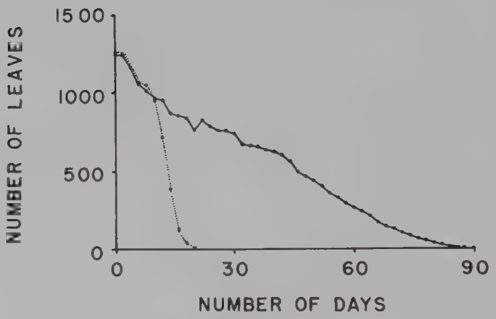


FIG. 7. The effect of relative humidity on the survival of excised stems of *P. smallii* over a period of 90 days. The broken line represents the total number of surviving leaves for 10 plants exposed to an atmosphere desiccated by calcium chloride and silica gel; the soil line for 10 plants in a saturated atmosphere.

week. At the end of the three-week period the "wet" plants failed to produce further reproductive units. The increased amount of flowering in the dry group may indicate that healthy plants subjected to severe desiccation may respond by flowering.

This experiment indicates the plants' ability to survive a prolonged water deficiency, but many of the uncontrolled experimental variables would lengthen or decrease the survival. Although diurnal fluctuations in temperatures are optimum for good growth, a constant temperature was necessary to prevent condensation. Light in the constant temperature room may have been too low for adequate photosynthesis. The duration of the experiment may have brought nutrient deficiencies into play.

Relative Drought Tolerance.—A group of 51 plants, all with 4 leaves, were selected from flats, transplanted to ceramic pots, and watered for a week so that their root systems were well established. The plants were then divided into groups of three plants each and treated according to a predetermined watering schedule. The control group was saturated with water every day. The 16 experimental groups received water in a graded series: group 1 receiving 26 cc of water every day, group 2, 26 cc every two days, group 3, 26 cc of water every three days, and continuing in this order so that the 15th group received 26 cc every 15 days. The 16th group, however, received 26 cc of water every 20 days.

Observations were made every three weeks on the growth of the plants. It was obvious from the beginning of the experiment that two distinct responses were elicited by the treatment. First, the plants which received less water exhibited a pronounced stunting; and second, their leaves turned a deep red shortly after the start of the treatment, while the others remained green. In addition, all plants which were watered less than every three days showed responses to the drought which they were undergoing by folding their leaves against the stems and sometimes leaves withered and dropped. After watering, the leaves expanded outward again for 3-4 days. Those plants which were watered less frequently than every 4 days resembled the plants in the field which were drought-stunted. The experiment was begun on July 2, 1957, and ended on October 30, 1957, for 121 days of the differential watering, almost a full growing season. Only three plants died during the treatment: one which was watered every 10 days, a second watered every 12 days, and a third watered every 20 days. Growth and branching occurred in those watered every 4 days or more frequently. Flowering occurred in all groups which were watered more frequently than every 15 days. Two plants survived 119 days with only 130 cc of water. Differential growth, flowering, and survival are shown in Table II.

TABLE II. Growth of plants after 4 months of differential watering

Watering Schedule*	Number of floral units			Number of leaves			Number of branches		
Saturated	75,	71,	80	118,	103,	106	9,	9,	8,
1.......	29,	31,	14	43,	51,	14	5,	6,	2,
2.......	10,	1,	3	11,	2,	7	0,	0,	0,
3.......	3,	1,	1	6,	3,	2	0,	0,	0,
4.......	38,	0,	0	49,	2,	3	4,	0,	0,
5.......	0,	1,	0	3,	3,	4	0,	0,	0,
6.......	1,	0,	1	3,	4,	2	0,	0,	0,
7.......	0,	2,	0	2,	5,	3	0,	0,	0,
8.......	1,	0,	0	3,	2,	4	0,	0,	0,
9.......	0,	0,	0	2,	3,	4	0,	0,	0,
10.......	2,	1,	dead	6,	4,	dead	0,	0,	dead
11.......	0,	1,	1	3,	3,	5	0,	0,	0,
12.......	1,	0,	dead	4,	3,	dead	0,	0,	dead
13.......	1,	1,	1	4,	2,	6	0,	0,	0,
14.......	0,	1,	1	2,	6,	4	0,	0,	0,
15.......	0,	0,	0	4,	4,	2	0,	0,	0,
20.......	0,	0,	dead	2,	3,	dead	0,	0,	dead

* The numbers in this column refer to the watering schedule explained in the text. Experimental groups were composed of three plants each.

Table II clearly emphasizes the depression of growth and its related processes with decrease in the available water. The aberrant response of one of the plants watered every 4 days and the death of three plants watered less frequently than 9 days indicates that there is a differential response of plants exposed to differing degrees of drought. The figure of 26 cc of water is misleading, since some of this water was lost through evaporation and was not available to the plants.

A second group of plants was also tested. These plants varied in age, but all were larger than the earlier experimental plants. The larger the plants (with increased transpiring surface area), the more they appeared to suffer from the drought conditions.

Inundation.—Five plants 6 weeks old were transferred from a flat to five 1,000 cc glass beakers on July 21, 1956. Soil was used to anchor the base of the plants. Water was added to the beakers so that only one inch of the plant remained above water, and this level was maintained by periodic additions of water. The soil did not have access to the atmosphere from the start of the experiment.

The lower portions of the plant lost their green color and lost some leaves after a short time. If, however, the water level fell below the tops of the lower branches, new green leaves were produced on them, indicating that the branch was still alive. These plants remained healthy and lived for eight months after the start of the experiment, while the control plants died three months earlier. Similar results were obtained in 1957.

P. smallii is well adapted to survive and reproduce in the extreme conditions present on the outcrops during the summer. Moisture is the most critical factor in the environment, controlling germination, establishment, and the vegetative growth and reproductive potentialities of the plant. Moisture is particularly important early in the life cycle and plants deprived of moisture either do not become established or fail to grow. Complete inundation will kill young seedlings. Partial inundation causes elongation; later these plants are more severely damaged from drought. After the plants become established they develop wide degrees of tolerance to different moisture conditions and are able to survive prolonged inundation or desiccation (Table II). Plants which are stunted early in life from lack of water do not recover and fail to make any appreciable growth even under optimum moisture conditions. When exposed to drought conditions, the plants develop the typical drought response with a change in pigmentation and withering and death of leaves.

Photoperiodism.—Experiments were conducted from July 15, 1956, to December 16, 1956, to ascertain the response of *P. smallii* to different photoperiods. The plants, which germinated from seeds given different photoperiods, were transplanted to ceramic pots. They were housed in a large light-tight box with five compartments when they were not exposed to light. The light-tightness of each of the compartments was checked by exposure of film strips over a twenty-four-hour period. The photoperiod for each group of plants was maintained by manual transfer of the plants from the light-tight sections to either daylight or the artificial light at night. The artificial light was turned on automatically at 2:00 a.m. each day and the plants were placed in such a way that they received 150 ft-candles of light or more at their apexes. Table III shows the time of exposure for the five groups of plants.

TABLE III. Photoperiod schedule

Group	Natural lighting	Artificial lighting	Light duration
A.........	8 AM to 4 PM		8 hours
B.........	8 AM to 6 PM		10 hours
C.........	8 AM to 2 PM	2 AM to 8 AM	12 hours
D.........	8 AM to 4 PM	2 AM to 8 AM	14 hours
E.........	8 AM to 6 PM	2 AM to 8 AM	16 hours

The number and types of floral units (buds, flowers, capsules, opened capsules, and capsules which had completely shed their seeds) and the number of leaves were counted every three days as a measure of the reproduction and vegetative responses to the treatment. Periodic surveys of height and branching supplemented these basic measurements.

The photoperiod had little effect on the germination of the seeds. After the macrosopic advent of the floral primordia, the plants exposed to a 10-hour photoperiod flowered in 5 to 8 days; 8-hour plants, 5 to 11 days; 12-hour plants, 7 to 12 days; 14-hour plants, 7 to 18 days; and the 16-hour plants, 7 to 18 days. The 10-hour plants bloomed earlier and had more total floral units than the other four groups. The 16-hour plants had the most vigorous growth, grew taller, had more leaves (although the leaves were smaller than the 10-hour plants), had more branches, and were the last to bloom. Figures 8 and 9 show the ratio of leaves to floral units for each of the groups.

Although the major effect of photoperiodism usually is found in formation of floral primordia it is interesting to note the comparative length of time it takes for the flowering process to be completed under different photoperiods.

In this latitude the maximum daylength is 14.6 hours and the minimum is 10 hours. The long photoperiod in the early life of the plant promotes vigorous vegetative growth. The photoperiodic response of the plant enhances the chances of flowering in nature, since it develops under conditions of decreasing duration of light approaching the optimum induction cycle of approximately 10 hours of daylight.

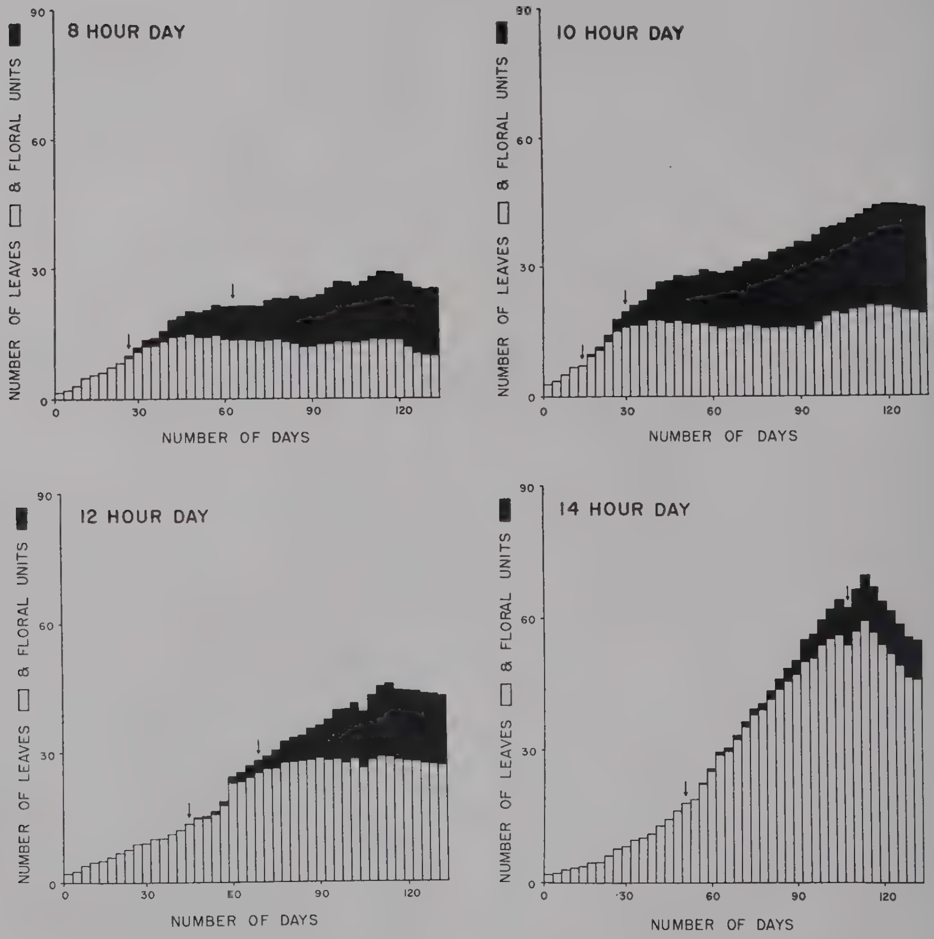


Fig. 8. The results of the photoperiod experiment. Each bar on these graphs represents the average for the measurement of 30 plants taken every three days for each of the experimental groups. The arrow on the left indicates the first appearance of flower primordia for each experimental group, and the arrow on the right indicates when all 30 plants in the experimental group had at least one flower bud. The number of hours exposed to light is indicated on each graph.

Light Intensity.—The effects of different levels of light intensity on the growth of *P. smallii* were tested by the use of cheesecloth screens which permitted penetration of certain percentages of light. Full light was considered to be the intensity of light received through the glass covering of the greenhouse on a bright summer day at noon. The other four groups received approximately the following fractions of that light intensity: 66%, 50%, 33%, and 25%. These fractions are based on the average of three measurements.

Groups of twenty seedlings, about the same size, were selected from flats in the greenhouse, transferred to each of the five experimental flats, and allowed one week to become established. The flats were then covered by layers of cheesecloth to give the desired light intensities.

Figures 10 and 11 show the effects of the different light intensities on the growth of the plants. Most of the plants which grew in the darkest exposure were killed or severely injured by an insect about one month after treatment began. Observations made on those plants before that time indicated that the trends established with regard to light intensity in the other four flats were exhibited to a greater extent in this flat. Plants which received less sunlight had fewer branches and sub-branches, larger but fewer

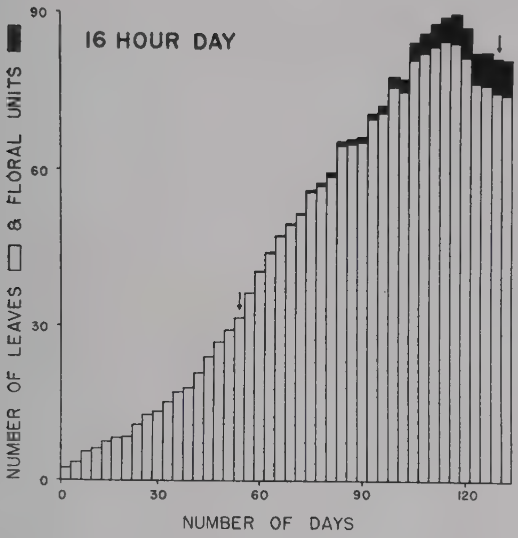


Fig. 9. The results of the photoperiod experiment, continued. Legend as for Fig. 8.

leaves, fewer floral units, and although they had longer stems their height was not as great as those in full light because there was a more prostrate or diffuse growth of these plants. There were no noticeable changes in the green pigmentation of the plants with the differences in light intensity.

Although there are differences in the growth of plants at different light intensities, the lowest light intensity tested did not prevent growth and flowering. The actual light intensity under the cheesecloth screens is considerably less throughout the day than the expressed percentage of full light measured at noon (Bormann, 1957). In the natural habitat *P. smallii* usually grows in full sunlight or partial shade in the morning or afternoon.

Responses to Light.—The flowers of *P. smallii* are only open for a short time around noon. They are also photocleistogamous and will not open if the light intensity does not exceed about 1500 footcandles. Photeolic movements were observed about dusk when the leaves fold upward, encompassing the main stem, and remain appressed in darkness. Young plants show a slight phototropic bending of the stems, but this is masked in the older plants due to the presence of branches. If the roots of the plant are exposed to light, they develop a red pigmentation.

Temperature.—The relationship between the germination of *P. smallii* and temperature has been mentioned in an earlier section. The significance of this critical relationship with germination is illustrated in the natural habitat and fully confirmed in the germination experiments in the laboratory. Observation of seedlings germinated in the greenhouse and constant temperature room indicates that a diurnal fluctuation in temperature is also necessary for establishment and good growth.

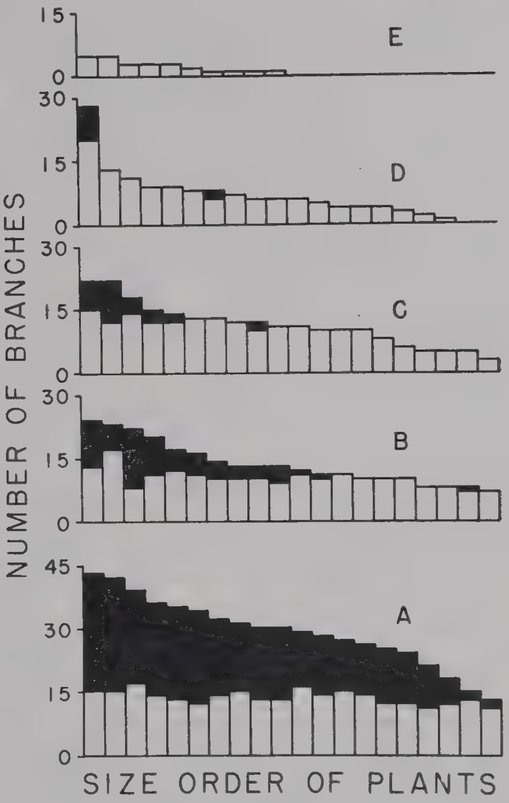


Fig. 10. The effect of light intensity on the branching of *P. smallii.* The 20 plants grown in each light intensity are arranged in order of the decreasing number of branches for convenience. The white bars represent the number of primary branches, and the black the number of secondary branches. A—full greenhouse light; B—66% full light; C—50%; D—33%; E—25%.

P. smallii will survive exposure to 0° C. for some time, but exposure to slightly lower temperatures results in death. Thus, low temperatures kill late survivors in the field and terminate the life cycle.

P. smallii demonstrates a remarkable ability to tolerate the high temperatures which occur on the outcrop during the summer. To determine the actual tolerance level of these plants, they were placed in pots in a circulating constant temperature bath and subjected to 40° C., 45° C., 50° C., and 55° C. for 15, 45, and 90 minutes. The results of this treatment are shown in Figure 12. Shortly after the plants were immersed in the

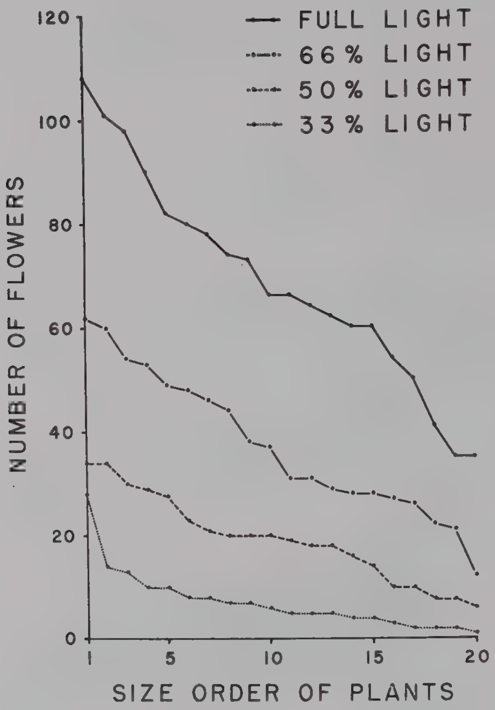
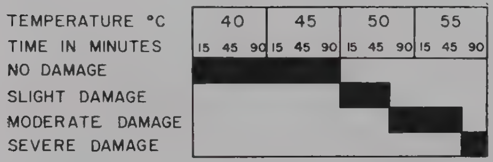


FIG. 11. The effect of light intensity on the number of flowers produced by *P. smallii* after two months of exposure to 4 different intensities. Plants have been arranged on the graph in descending order of flower number.



TEMPERATURE °C	40			45			50			55		
TIME IN MINUTES	15	45	90	15	45	90	15	45	90	15	45	90
NO DAMAGE	■	■	■	■	■	■						
SLIGHT DAMAGE							■	■				
MODERATE DAMAGE									■	■	■	
SEVERE DAMAGE												■

FIG. 12. Temperature tolerance of *P. smallii* as determined by exposure of plants to given temperatures for specified times in a constant temperature bath. Slight damage refers to blanching of one or two leaves, and severe damage to the destruction of all but one or two of the youngest leaves. Lethal temperatures for the whole plant were not reached.

water bath, the leaves folded up, protecting the inner young leaves and the bud. The first sign of damage was a blanching of the outer leaves. The more severe damage increased the number of leaves affected. At 55° C. for 90 minutes, most of the leaves were affected but occasionally a few young leaves survived. The stem was not damaged in any of the treatments.

A diurnal fluctuation in temperature is optimum for best growth. *P. smallii* shows little resistance to cold and is killed by short exposures to sub-freezing temperatures. It survives exposure to temperatures up to 55° C. and lethal temperatures were not reached in the experiment. The leaves respond to high temperatures by folding against the stem, thus protecting the younger leaves and the bud. Young leaves and the stem show the greatest resistance to heat, although the protection of the older leaves may decrease the effective heat exposure.

Competition.—Four groups of ten plants were transplanted to four ten-inch pans. Rye seeds were heavily sown in two of the pans to test the effect of competition on the growth of *P. smallii.* Observations on height, branching, number of leaves, and reproductive activity of the plants were made each week for a period of four months.

The plants grown under competition with rye were at first taller but later failed to keep up with the growth of the controls. The control plants attained a greater final height, bloomed first, and had more flowers, leaves, and branches. Plants on the outcrops show similar growth patterns to the plants grown with rye when they are found under heavy vegetation. They are tall, erect plants with few leaves and branches.

Competition is probably the major factor limiting the spread of this plant to other areas. On the outcrop the adverse environmental conditions prevent serious competition from other plants. *P. smallii* grows in an isolated area and the associated plants seldom attain densities high enough to interfere with its growth.

SUMMARY

Portulaca smallii is a small succulent annual sporadically occurring but endemic to the granite outcrops of the Piedmont Plateau of the southeastern United States. Primarily it occupies a narrow band of soil on the edge of the outcrops in an ecotone between the exposed granite and the surrounding marginal vegetation. It often occurs in the rock rubble of past quarrying operations and less frequently in other habitats on the outcrops. Transplant quadrats demonstrated the ability of the plant to occupy areas of the outcrop where it does not grow at present, but the only indication of aggressive invasion on an outcrop habitat is in the rock rubble areas. There is no evidence that it is extending its range.

The only plants occuring frequently enough in this restricted habitat to be considered as associates of *P. smallii* are *Talinum teretifolium, Cyperus granitophilus,* and *Stenophyllus capillaris.* The plant is rarely found growing in dense competition. The biotic influence comes mainly from insects which feed on the plants.

P. smallii grows in the extremes from saturated and even inundated soil to completely air dry soil but occurs optimally in the intermediate ranges.

P. smallii germinates in late June or early July with flowers first appearing toward the end of July, and capsules with ripe seeds a week later. Flowering continues through most of the growing season and is followed by a senescent period marked by decreased physiological activity and tolerance. Variations in the timing of the physiological events within the population may be due to either the innate properties of the different plants or the differences in the microenvironment. Phenological variation from year to year is governed by the climates for each growing season.

Observations on 12 outcrop populations revealed morphological variations for each which exceeded the described limits of the species. Many of the morphological expressions, particularly those relating to size or growth responses, could be directly related to the environment; but others, such as floral variation, defied ecological explanation. The vegetative and physiological variations are controlled by both the innate genetic characters of the plant and the environment. On the basis of such data, *P. smallii* appears to merit a specific rank, but it is very closely related to *P. pilosa* and there is an overlap in the characteristics which distinguish them. The increased overall size and number of stamens in *P. pilosa* and the endemism of *P. smallii* are the best clues for distinguishing these plants.

Germination of the seed is prevented by the impermeability of the testa. Seeds could be germinated in the laboratory by breaking the testa, thus making plants available for study throughout the year. Seedling establishment is the most critical phase of the life cycle. Water is essential for good establishment and greatly affects the growth and vigor of the mature plants.

Plants deprived of optimum moisture develop a typical drought response. Prolonged drought prevents growth, delays flowering and brings about a typical red pigmentation, followed by withering, leaf drop and death.

The flowers of *P. smallii* are photocleistogamous and are open for only a short period about noon. Plants are also phototropic and exhibit photeolic movements. *P. smallii* is photoperiodic, the optimum induction cycle being slightly less than 10 hours. Decreased light intensity causes a reduction in growth and flowering of the plants.

Other factors which are significant in its growth are its self and cross pollinated flowers and the lack of a specific adaptation for seed dispersal.

P. smallii appears to be well adapted to its environment. The requirement of high light intensities, the need for freedom from competition, its tolerance to high temperatures and extreme moisture conditions not only account for its ability to live under the extreme outcrop conditions, but also account for its strict endemism.

REFERENCES

Baker, W. B. 1945. Studies of the flora of the granite outcrops of Georgia. Emory University Quarterly **1:** 162-171.

———. 1956. Some interesting plants on the granite outcrops of Georgia. Georgia Mineral Newsletter **9:** 10-19.

Bouyoucos, G. J. 1937. A sensitive hydrometer for determining small amounts of clay or colloids in soils. Soil Sci. **44:** 245-246.

Bormann, F. H. 1956. Percentage light readings, their intensity—duration aspects, and their significance in estimating photosynthesis. Ecology **37:** 473-476.

Guptill, P. L. 1941. The morphology and life cycle of *Talinum teretifolium* Pursh. M.S. Thesis, Emory University Library.

Harper, R. M. 1939. Granite outcrop vegetation in Alabama. Torreya, **39:** 153-159.

Herrmann, L. A. 1954. Geology of the Stone Mountain—Lithonia District. Geological Survey, Bull. No. 61, 139 pp.

Johnson, M. 1938. Studies in the life cycle of *Isoetes melanospora.* M.S. Thesis, Emory University Library.

Keever, C. 1957. Establishment of *Grimmia laevigata* on bare granite. Ecology **38:** 422-429.

———, **H. J. Oosting, and L. E. Anderson.** 1951. Plant succession on exposed granite of Rocky Face Mountain, Alexander Co., N.C. Bull. Torrey Bot. Club **78:** 401-421.

Kilmer, V. J. and L. T. Alexander. 1949. Methods of making mechanical analyses of soils. Soil Sci. **68:** 15-25.

Lunsford, D. E. 1939. Studies on the life cycle of *Amphianthus pusillus* Torr. M.S. Thesis, Emory University Library.

Lyon, T. L., H. O. Buckman, and N. C. Brady. 1952. The nature and properties of soils. New York, The Macmillan Co., 590 pp.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1951. American Wildlife and Plants. New York, McGraw-Hill Book Co. 394-395.

Mathews, J. 1941. A survey of the flora of Mount Panola. M.S. Thesis, Emory University Library.

McCranie, E. J. 1938. Studies in the life cycle of *Diamorpha cymosa.* M.S. Thesis, Emory University Library.

McVaugh, R. 1943. The vegetation of the granite flat-rocks of the southeastern United States. Ecological Monog. **13:** 119-166.

Oosting, H. J. and L. E. Anderson. 1937. The vegetation of a barefaced cliff in western North Carolina. Ecology **18:** 280-292.

———. 1939. Plant succession on granite rock in eastern North Carolina. Bot. Gaz. **100:** 750-766.

Platt, R. B. and J. P. Witherspoon. Ecological effects of radiation on selected natural environments: II. Preliminary studies on plant populations and communities. MS.

Small, J. K. 1933. Manual of the southeastern flora. Chapel Hill, The University of North Carolina Press, 1554 pp.

Smith, M. L. M. 1938. A study of the flora of Stone Mountain and vicinity. M.S. Thesis, Emory University Library.

Speer, V. L. 1942. A study in the life history of *Gelsemium sempervirens* (L.) Ait. F. M.S. Thesis, Emory University Library.

Steiner, E. 1944. Cytogenetic studies on *Talinum* and *Portulaca.* Bot Gaz. **105:** 374-379.

Stipe, M. S. 1939. Studies in the life cycle of *Sabulina brevifolia* (Nutt.) Small. M.S. Thesis, Emory University Library.

Watson, T. L. 1902. Granites and gneisses of Georgia. Geological Survey of Georgia Bull 9-A, 367 pp.

Whitehouse, E. 1933. Plant succession on central Texas granite. Ecology **14:** 391-405.

Wiggs, D. N. 1956. Studies on the ecological life history of *Diamorpha cymosa* (Nutt.) Britton. Ph.D. Dissertation, Emory University Library.

Wilson, P. 1932. *Portulaca.* North American Flora **21:** 228-236.

INTERPRETATION OF LOOP-FREQUENCY DATA AS A MEASURE OF PLANT COVER

SELAR S. HUTCHINGS AND RALPH C. HOLMGREN
Intermountain Forest and Range Experiment Station, Forest Service,
U. S. Department of Agriculture, Ogden, Utah

Small plots are often used to measure occurrence or frequency of plant species. Such measures, and the mathematical relation between plot size, plant numbers, and plant distribution have been evaluated by various investigators, including Aberdeen (1958) and Curtis and McIntosh (1950). However, frequency data obtained from small circular plots are being used as indices of percent basal area or plant cover. Without full recognition of the inherent bias and mathematical relations involved, such data may easily be misinterpreted.

An example of the use of frequency data in measuring changes in plant cover on grazing allotments is one phase of the "3-step method" described by Parker (1950, 1951). The first step of this method consists of recording, summarizing, and interpreting frequency data from a series of circular plots three-fourths of an inch in diameter circumscribed by a metal ring or loop. These are located at 1-foot intervals along permanently established transects, ordinarily 100 feet long. Presence of perennial vegetation is recorded by species whenever any portion of the base or crown, as appropriate, occurs within the plot. The percent of plots containing perennial vegetation is designated "plant-density index" or "loop-density index"; the latter term is used in this article. The index serves as a bench mark with which subsequent observations can be compared to determine trend or change in range condition. Parker was aware that this procedure was not an actual measure of plant cover, but assumed it to provide a reliable index.

In reference to terminology, "plant density" warrants further comment. Some technicians use this term to indicate percent ground cover, either basal or aerial, while others use it to refer to number of plants per unit area. To avoid confusion we have adopted "percent plant area" to designate the proportion of ground surface covered by vegetation, and "number of plants per unit area" for density in its other sense.

Parker (1950, 1951), Johnston (1957), Sharp (1954), and Short (1953) have evaluated various features of the loop-index method, its variability in sampling plant area, its sensitivity in detecting changes in percent plant area, and sampling intensity requirements for statistical control. Also, some of these writers have suggested modifications to improve the measuring technique. These aspects are relatively incidental to the present discussion. The second and third steps of the 3-step method, which provide supplemental information, do not pertain to the point of discussion.

The purpose of this paper is to point out the theoretical relation between the loop-density index and acual percent plant area, and to discuss the effects of plot size, number and size of plants, plant distribution, and plant shape on these indices. Results of tests on synthetic and natural plant populations illustrate theoretical relations and suggest modifications for correcting the bias of loop-density indices..

Theoretical Considerations

Plot Size

The ¾-inch loop described by Parker (1951) as a "point of dimension" was a compromise between a point where only the presence or absence of vegetation is recorded and a larger plot where percent cover is estimated. In using the loop, data are recorded in the same manner as in the point-intercept method described by Levy and Madden (1933). If actual points were used and enough samples taken to make sampling error negligible, the percent of points occupied by plants would approximately equal the actual percent plant area. Since the ¾-inch plot has area, however, it overrates plant cover. This was pointed out by Parker (1950), but the nature of the bias was not fully investigated.

Several other workers have also demonstrated this relation. Winkworth (1955) in heathland obtained a reading of 117.5 percent aerial plant cover (includes overlap of different species) by observing 200 points. When he increased the diameter of the "points" to 1.83 mm he recorded 193.5 percent cover. Goodall (1952), using pins 0, 1.84, and 4.75 mm thick, showed progressive overestimation of vegetation as pin size increased. Curtis and McIntosh (1950), in sampling a synthetic plant population, found that recording plants when only a fractional part fell within plots "gave over-representation, particularly of the more numerous species."

When the sampling unit has area, as in the loop-frequency method, it will include plants, or parts of plants, that would be missed by a point at its center. Plant "hits" will occur whenever the plot center falls within a peripheral zone equal in width to the radius of the plot. Thus, a positive bias is introduced. The bias in the loop-density index, then, is due to the enhancement of actual plant area by a supplementary area: that of a border the width of the loop radius surrounding each plant.

Size and Number of Plants

Parker (1950) plotted loop-density index, pace-transect, and frequency-point data against percent plant area obtained by the line intercept. These three methods gave higher values than the line-intercept method of Canfield (1941); the data presented showed a linear relation between the methods. Therefore Parker concluded that all three methods gave good indices of percent plant area. However, the relation between percent plant area obtained by the line-intercept method is not always linear with loop-density index. Johnston (1957) compared the line-intercept, vertical-point-quadrat, and loop-frequency techniques. Data from the line-intercept and vertical-point-quadrat methods were approximately the same; but the loop-frequency method overrated vegetal cover for all species and all sites. The ratios of the index to plant area in Table I, adapted from Johnston's paper, illustrate this point.

Table I. Ratios of the loop-density index to basal area measured by line-intercept (adapted from Johnston (1957))

Species	Sampling Locations		
	Coalhurst	Lethbridge	Vauxhall
Agropyron smithii	4.90	4.29	3.75
Bouteloua gracilis	2.26	2.03	2.02
Carex spp.	8.01	4.32	7.18
Poa secunda	....	2.71	4.00
Stipa comata	3.58	1.99	1.62

The values in Table I are conversions from loop indices and were derived by dividing loop-frequency indices of vegetal cover by the percent plant area obtained with the line-intercept method. The loop-density index in these samples overestimated percent plant area from 1.62 to 8.01 times as compared to results from the line-intercept method. The amount of overestimation is not linear for species, total plant cover, or location, but seems to be associated to some degree with growth characteristics of the various species. Single-stemmed plants or plants having small area are most highly overrated.

The disortion or bias inherent in the loop method, as affected by size of plants, can be computed mathematically if certain characteristics of the vegetation are known. The percent of an area occupied by all plants is the sum of the percentages of the area occupied by individual plants. If the plants are circular, then the percent of area occupied by all plants, y, is shown by the equation:

$$y=\frac{\sum_{p=1}^{n} 100\pi r_p^2}{A}, \tag{1}$$

where n is the number of plants present, r_p the radius of plant p, and A is the total ground area.

Using a circular plot of any diameter and recording a hit when only a portion of the plot is occupied by plants gives an index value x greater than actual basal area y. This can be computed by

$$x = \frac{\sum_{p=1}^{n} 100\pi(r_p + r_1)^2}{A}, \tag{2}$$

where r_1 is the radius of the plot or loop used to sample the vegetation. The bias b, or number of times the loop index is greater than the percent plant area, is

$$b = \frac{x}{y}. \tag{3}$$

With a constant plot size, such as a three-fourths inch loop ($r_1 = 0.375$), the bias varies with plant size. It decreases as plant size increases and approaches unity for large plants (Fig. 1). For plants having a radius of one-sixteenth inch the loop-density index is 49 times the actual percent plant area. For plants with radii of three-eighths inch, 1 inch, and 5 inches, the ratios are 4.0, 1.9, and 1.2, respectively. The bias changes relatively little for plants having radii greater than 2-½ inches. The line at bias = 1 in Figure 1 is asymptotic to the bias curve.

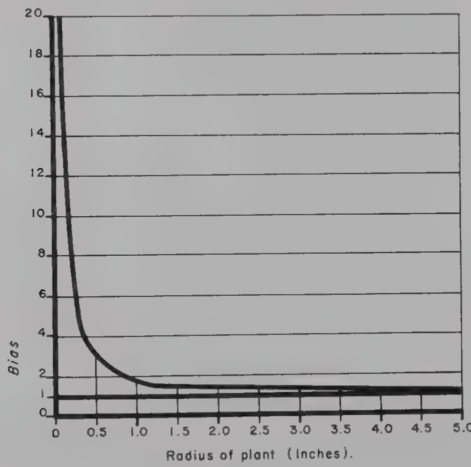


FIG. 1. Effect of plant size on the bias of the loop-density index obtained with a ¾-inch loop.

Plants of equal size.—Where all plants are circular in shape and equal in size, r_p is constant and the bias b becomes

$$b = \left(\frac{r_p + r_1}{r_p}\right)^2. \tag{4}$$

In such populations, percent plant area y and loop-density index x will vary with plant numbers n per given area A as follows

$$y = \frac{100n\pi r_p^2}{A}, \tag{5}$$

and

$$x = \frac{100n\pi(r_p + r_1)^2}{A}. \tag{6}$$

From these equations a set of comparisons of expected loop-density indices with percent plant area were computed for 22 theoretical populations of circular plants. These are given in Table II. The bias given in the right-hand column of the table is that plotted in Figure 1. For such plant populations it is apparent from the table that indices can be converted to actual percent plant area if either of two values is known: number of plants per unit area n/A, or size of plant r_p.

TABLE II. Comparative values of percentage plant area (y) (upper figure of each pair) and expected loop index (x) (lower figure of each pair) for 22 theoretical populations of circular plants

Radius of plant (r_p)	PLANT AREA		NUMBER OF PLANTS PER SQUARE FOOT			Bias
	Actual	Theoretical[1]	1	3	5	
In.	*Sq. in.*	*Sq. in.*	*Percent*			
0 (point)	0.0	0.4418	— 0.31	— 0.92	— 1.53	∞
1/16	.0123	.6013	.0085 .42	.0256 1.25	.0426 2.09	49.0
1/8	.0491	.7854	.034 .55	.102 1.64	.170 2.73	16.0
3/16	.1104	.9940	.08 .69	.23 2.07	.38 3.45	9.0
3/8	.4418	1.7671	.31 1.23	.92 3.68	1.53 6.14	4.0
1	3.1416	5.9396	2.18 4.12	6.55 12.37	10.91 20.62	1.9
2	12.5664	17.7205	8.73 12.31	26.18 36.92	43.63 61.53	1.4
5	78.5398	90.7626	54.54 63.03	— —	— —	1.2

[1] Adjusted for 3/4-inch loop.

If number of plants per unit area is known, percent plant area can be derived from recorded loop indices by:

$$y = \left(\sqrt{x} - \sqrt{\frac{100n\pi r_1^2}{A}}\right)^2. \tag{7}$$

Curves of this equation are shown in Figure 2, where each curve is for a constant number of plants per unit area. Changes in percent plant area due only to changes in plant size result in this curvilinear relation of the loop-density index to percent plant area.

If plant size is known, percent plant area can be derived from the indices by:

$$y = \frac{x r_p^2}{(r_p + r_1)^2}. \tag{8}$$

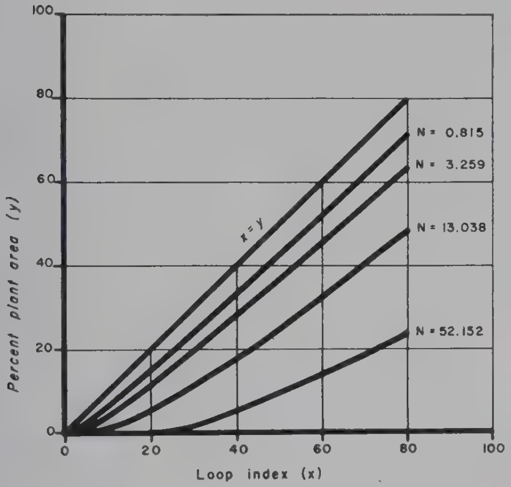


FIG. 2. Relation of loop-density index to percent plant area for given sizes of plants (r_p), expressed in inches. The relations are for theoretical populations of circular plants of uniform size.

Curves of this equation are shown in Figure 3, where each line is for a constant size of plant. Changes in percent plant area due only to changes in number of plants present result in this straight line relation of loop-density index to percent plant area.

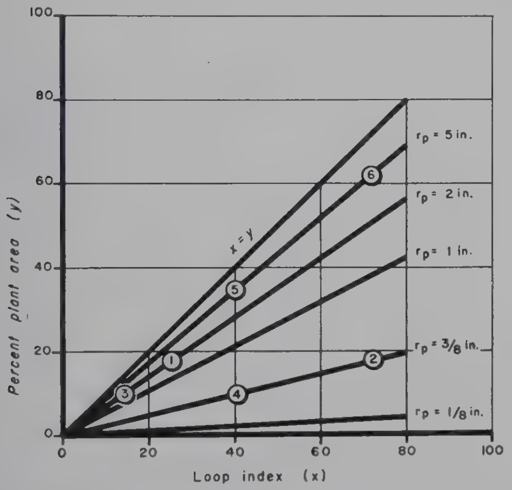


FIG. 3. Relation of loop-density index to percent plant area for given sizes of plants (r_p), expressed in inches. The relations are for theoretical populations of circular plants of uniform size.

Six numbered points in Figure 3 illustrate how the relation between loop-density index and percent plant area is affected by plant size and number. Statistics for the indicated populations are given in Table III. This table demonstrates that loop indices of 25 and 72 can both be obtained from plant populations that provide only 18% actual ground cover. A loop-density index of 72% can represent actual cover varying from less than 18% to more than 62%. Depending on size and number of plants, the loop-density index may range from slightly more to many times more than the actual percent plant area.

TABLE III. Statistics for the six populations indicated by the numbered points in Figure 3

Population	Plant radius	Plants per square foot	Actual cover	Loop index
	Inches	Number	Percent	Percent
1	2.000	2.1	18	25
2	.375	58.7	18	72
3	2.000	1.2	10	14
4	.375	32.6	10	40
5	5.000	.6	35	40
6	5.000	1.2	62	72

Plants unequal in size.—Natural plant populations in which the individuals have uniform size are relatively rare. Usually plants vary greatly in size, and size classes are often skewed. For a population of circular plants unequal in size, conversion of loop-density index to percent plant area can be made if both the mean radius $\bar{r}_p$ and number of plants per unit area n/A are known:

$$y = x - \frac{100n\pi}{A}\left[(\bar{r}_p + r_1)^2 - \bar{r}_p^2\right]. \tag{9}$$

A closer approximation of percent plant area could be computed from n/A and r_p without making loop readings.

Plant Distribution

Loop-density indices, and consequently their conversion to actual basal area, are also influenced by plant spacing or distribution.

In using the loop-frequency method, if more than one plant (or parts of more than one plant) is found in a plot, the "hit" is given a recorded value of 1. If more than one species is present they are given equal fractional values. In an ideal population of circular plants, all of the same size, a further qualification is required if the expressions of y in terms of x (Figs. 2 and 3) are to be valid. Recording "multiple hits" in the same manner as hits on single plants reduces the bias x/y, so that the relations described above for circular plants must be qualified when plants are closer together (edge to edge) than the diameter of the plot $2r_1$. If plot readings are weighted by the number of plants (that occur wholly or partially) within the plot, the relation of the loop-density index to percent plant area would be given by equations (7) and (8). The spatial distribution of plants, whether systematic, random, or contagious, has no effect on the bias unless some plants happen to be close enough together to result in multiple hits.

In Figure 4, one of the curves from Figure 2 has been replotted to illustrate the effect of plant spacing on loop-density indices where plot observations are not weighted as suggested above.

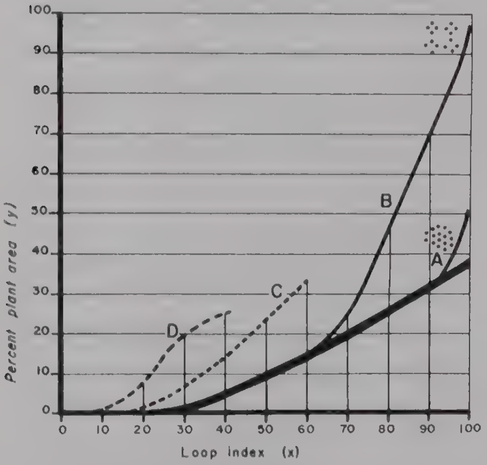


FIG. 4. Relation of loop-density index to percent plant area in theoretical populations of circular plants, all of the same size, but with a constant number of 52 plants per sq. ft. Departures from the heavy curve are for populations in which some plants are less than ¾-inch from others. Departures A and B are for systematic patterns as shown. Departures C and D are approximations of the relation for random and grouped populations, respectively.

The two solid curves rising from the original curve represent systematic arrangements; curve A represents plants located on corners of equilateral triangles and equidistant from six other plants, and curve B represents plants located on corners of octagons and equidistant from three others. Curve C roughly approximates the relation of percent plant area to loop-density index for a random plant arrangement, and curve D approximates the relation for some irregular spacing in which plants tend to be in groups. The linear relations shown in Figure 3 would have to be adjusted similarly for irregular plant distributions where minimum edge-to-edge distance between plants is less than the diameter of the plot used.

Shape of Plants

The foregoing considerations are based on the assumption that plants are circular in outline. Irregularity in shape and compactness of plants introduce other variables, and as plants depart from circularity the discrepancy between loop-density index and actual percent plant area increases. This is illustrated by the diagrams in Figure 5, where all four shapes have equal area.

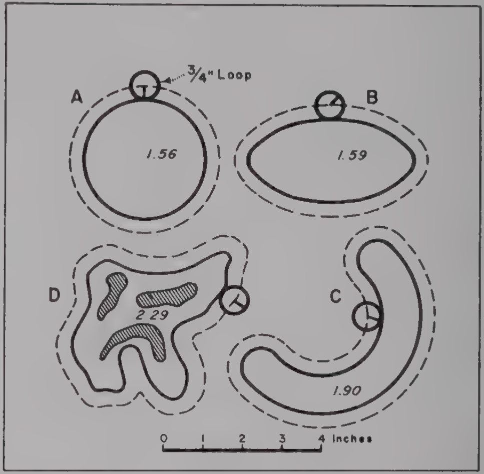


FIG. 5. Effect of plant shape on the ratio of loop-density index to actual percent plant area. Each figure ("plant") has an area of 7.0686 square inches. Ratios are given in each figure.

The bias x/y is given in each figure. Obviously the bias is related to plant perimeter, but plant area is also involved, since plants with equal perimeters can have unequal areas. Basal area of irregularly shaped plants that have openings within the crowns such as shown in Figure 5D are most overrated by loop-density index.

TESTS WITH SYNTHETIC PLANT POPULATIONS

Synthetic populations of circles were constructed on two strips of paper 60 feet long by 2 feet wide. On one of them the circles were 29/32 inch in diameter, each containing a concentric circle ⅜ inch in diameter. On the other were 4-inch circles with concentric 2-inch circles. The centers of circles were located by paired random numbers, and although the larger circles on each paper could be tangent to others none were allowed to overlap. The circles were of various colors, so that by using different color combinations it was possible to sample populations having different mean numbers of plants per square foot.

Loop-density indices were obtained from these synthetic plant populations by sampling with a loop having a diameter of 13/16 inch ($r_1 =$ 0.40625). A "cluster" of sixteen randomly located, 50-foot loop-transects, 800 loop readings, constituted a sampling unit. Samples were composed of from 8 to 33 units. In addition, the loop-density indices were compared with rated loops on the populations of ⅜-inch and 29/32-inch circles. The loops were rated to the nearest 10%, as to the portion covered by the synthetic vegetation represented by the circles.

Loop-density indices from several of the synthetic populations are shown in Table IV with percent "plant area" and expected indices computed by equation (6), shown for comparison. The latter agree rather closely with the indices obtained by sampling, except for the denser populations of 4-inch circles, where many individuals were tangent to others, and sample plots sometimes included parts of two circles.

Table IV. Actual and theoretical indices of samples from 18 synthetic populations of circles sampled by the loop-frequency[1] method

Diameter of circle	Circles per square foot	Area occupied by circles	Loop index	Bias	Expected Indices: Adjusted for plant size and number	Expected Indices: Adjusted for close spacing
Inches	*Number*	*Percent*	*Percent*	*Ratio*	*Percent*	*Percent*
3/8	3.0	0.2301	2.6706	11.6	2.3074	—
29/32	3.0	1.3438	4.9167	3.7	4.8393	—
2	1.0	2.1817	4.1719	1.9	4.3143	—
	1.5	3.2725	5.7344	1.8	6.4715	—
	2.0	4.3633	8.3438	1.9	8.6286	
	2.5	5.4542	9.9063	1.8	10.7858	—
	3.0	6.5450	11.4688	1.8	12.9430	—
	5.0	10.9083	19.8126	1.8	21.5716	—
4	1.0	8.7266	12.3281	1.4	12.6319	12.4228
	1.5	13.0900	16.9844	1.3	18.9479	18.5894
	2.0	17.4533	23.9562	1.4	25.2638	24.3505
	2.5	21.8166	28.3125	1.3	31.5798	30.4019
	3.0	26.1799	32.4688	1.2	37.8957	36.2911
	5.0	43.6332	55.1875	1.3	63.1595	58.2943

[1] Theoretical expected values are computed for 13/16-inch diameter loop used in sampling.

The expected indices for 4-inch circles were adjusted to compensate for the known tangential contacts in that population. The adjusted values (final column Table IV) are somewhat nearer the loop indices from the sampling than are the expected indices computed without regard to plant spacing. The remaining discrepancies between the loop-density indices from sampling and those theoretically expected must be attributed mainly to sampling error.

Rated loops provided close estimates of the actual percent area covered by artificial populations of ⅜-inch and 29/32-inch circles, being 1.2 and 1.1 times greater than the actual for the two populations, respectively (Table V). Loop-density index values overrated the area of the ⅜-inch circles 11.4 times and the 29/32-inch ones 3.8 times. However, when the loop-density indices were adjusted for "plant" size, using equation (7), very close estimates of the actual percent area covered by the artificial populations were obtained, the ratios of observed to known and expected being 1.14 and 1.05, respectively, for the two sizes of circles. These close estimates resulted because all "plants" were equal in size and circular; in this case the adjustment accounts for almost all of the bias.

Table V. Estimates of percent "plant" area on synthetic, randomly distributed "vegetation" (circles) obtained from loop-density indices and rated loops[1]

	3/8-INCH CIRCLES: Loop index	3/8-INCH CIRCLES: Rated loops	29/32-INCH CIRCLES: Loop index	29/32-INCH CIRCLES: Rated loops
	1.250	.1500	1.625	.7125
	.625	.1125	1.250	.5500
	.875	.0625	1.375	.4500
	.500	.0625	1.875	.4500
	.875	.0500	1.500	.3125
	1.500	.1625	2.500	.8750
	.500	.1375	1.750	.6375
	.375	.1125	1.875	.5625
	.875	.0875	1.750	.3375
	1.125	.0250	2.500	.3125
	1.000	.1125	1.750	.5875
	1.125	.0875	1.375	.3875
	1.000	.0875	1.250	.3375
	.500	.0875	1.250	.5125
	1.000	.1625	1.750	.6250
Average (percent)	.8750	.0900	1.6917	.5100
Actual area (percent)	.0767	.0767	.4479	.4479
Bias (ratio)	11.4	1.2	3.8	1.1
Coefficient of variation	36.6	54.4	20.6	32.1

[1] Data are averages of 800 13/16-inch loop readings.

The estimates of percent plant area by the rated and unrated loops were extremely variable for these two populations of small-sized individuals; they were most variable for the rated loops and for the smallest circles.

Tests with Natural Plant Populations

Winterfat

Loop-density indices of shrub-crown area were obtained from eight 100-foot transects in each of 14 winterfat (*Eurotia lanata*) stands. Winterfat was selected for study because the low shrubs are rather compact, often uniform in size, and tend to be somewhat circular in outline. Sampling sites were limited areas (1 to 2 acres) throughout which the stand appeared to be uniform as to size, number of plants, and distribution pattern; but the separate sites were selected so as to provide wide variation in number and size of plants between stands. At each sampling site plant counts were made on forty 10-square-foot plots, and on each of these the crown area of four plants selected at random was determined by measuring the average radius, disregarding small openings in the plant crowns or irregularity of outline. This provided a comparative measure of plant area.

Loop-density indices obtained from the 14 winterfat stands did not provide consistent estimates of percent plant area. The loop-density indices varied considerably, but on every stand were higher than the measured plant area (Table VI).

Table VI. Loop-density indices of winterfat stands compared with plant area and expected indices computed from numbers and size classes of plants found within the populations

Stand number	Plant area[1]	Loop index	Expected index	Average plant size	Plants per square foot	Bias
	Percent	*Percent*	*Percent*	*Sq. in.*	*Number*	*Ratio*
1	3.4	5.3	6.9	2.20	2.23	1.56
2	4.1	7.8	5.4	8.91	.67	1.88
3	4.7	6.5	6.4	13.82	.49	1.47
4	6.6	11.3	10.6	5.66	1.69	1.71
5	6.9	9.8	11.5	3.94	2.54	1.42
6	7.5	8.0	10.2	13.31	.81	1.07
7	9.4	14.1	13.2	10.89	1.24	1.50
8	11.0	12.3	13.4	24.81	.64	1.12
9	11.9	15.0	14.7	30.69	.56	1.26
10	12.1	20.9	19.2	5.56	3.14	1.73
11	13.2	15.3	18.4	10 90	1.75	1.16
12	16.9	33.7	28.4	4.19	5.80	1.99
13	18.6	20.6	24.1	19.99	1.34	1.11
14	21.6	24.3	27.2	23.49	1.32	1.13

[1] Derived from array of plant sizes as measured on a series of 10-sq.-ft. plots.

However, expected loop-index values computed from plant number and size classes found within the winterfat stands agree closely with the actual index values obtained by sampling.

The expected indices shown in the table were computed from plant numbers per unit area and mean plant radius by a form of equation (9),

$$x = y + \frac{100 n \pi}{A}\left[(\bar{r}_p + r_1)^2 - \bar{r}_p^2\right]. \qquad (10)$$

Although all values were influenced by sampling error, apparently the major factors affecting loop-density indices, are variability in plant number, plant size, and plant shape. Undoubtedly plant distribution or spatial arrangement of plants, i.e., proximity to other plants, also influenced the loop-density indices.

Wheatgrass, Balsamroot, and False-Toadflax

A study by Smith[1] on the Upper Snake River Experimental Range near Dubois, Idaho, also illustrates the effects of plant number and size on loop indices (Table VII). He obtained plant numbers and basal area from a 100-percent inventory of eight 75-square-foot plots on which he determined loop-density indices for three species from 1,600 loop observations.

Table VII. Characteristics of three plant populations on sagebrush-grass range, and actual and expected hits per 100 for a ¾-inch loop

	Wheatgrass	Balsamroot	False-toadflax
Total plant number	2,329	272	249
Total root crown area (sq. cm.)	4,641	6,320	24
Average size of plant (sq. cm.)	1.99	23.24	.09
Actual basal area (percent)	.83	1.13	.004
Loop-density index (hits per 100)	5.95	2.70	.06
Expected loop-density index[1]	3.19	2.10	.18

[1] Computed from number and size of plants found within the populations by equation (2).

The total basal area of wheatgrass (*Agropyron spicatum*) in these eight plots was 27% less than that of balsamroot (*Balsamorhiza sagittata*), but its loop-density index was more than twice as great. There were nearly nine times as many wheatgrass as balsamroot plants, but their average area was only one-twelfth as large. The relative index values support the theory that for a given percent plant area, populations of many small plants give a greater loop-density index than populations of fewer large plants.

The expected hits were computed by correcting the array of plant sizes found in the populations by the radius of the loop as given in equation (2). For this computation all plants were assumed to be circular. The expected loop-density index of 3.19 for wheatgrass (Table VII) was 46% low; and balsamroot, with 2.10, was 23% low. Discrepancies between the observed and expected values are probably due mainly to departures of plants from circularity and partly to sampling error. Examination of quadrat charts from the Upper Snake River Experimental Range showed wheatgrass to be the most irregular in outline of the three species. Elongated, crescentic, and odd-shaped plants were the rule rather than the exception.

Although there were 249 false-toadflax (*Comandra umbellata*) plants on the sampled area, nearly as many as of balsamroot, only one hit was recorded from 1,600 loops. This may seem odd, but false-toadflax plants were small and single-stemmed and had an average basal area of only 0.09 sq. cm. The mean spatial area per plant is 2,238 sq. cm., 800 times the loop area. Assuming random distribution, the expected loop-density index is much less than 1 percent and, to this extent, the results accord with theory.

---

[1] Smith, Justin G. 1958. An appraisal of the loop transect method of estimating vegetal changes based on root crowns. Unpublished manuscript, Intermountain Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Ogden, Utah.

Mountain Brome

Size, shape, number, and distribution pattern of plants often change from year to year as ranges deteriorate or improve. This is illustrated by photographs and mapped charts of quadrats made over a period of years on summer ranges on the Manti National Forest in central Utah. The ability of the loop-frequency method to detect real changes was tested by sampling a series of charts, all from a single quadrat that was mapped eight times between 1932 and 1953. For simplicity of testing, changes in a single species, mountain brome (*Bromus carinatus*), were followed. Four hundred circular ¾-inch plots reduced to chart scale were located in the same positions on each of the eight charts.

The quadrat charts may not provide precise representation of plant sizes and numbers because they are undoubtedly influenced by pantograph equipment, personal errors, etc. However, they illustrate the effect that plant sizes and plant numbers as mapped have on loop-density indices.

In 1932, when the quadrat was first charted, a total of 32 plants—18 large and 14 smaller ones—were scattered over the area. In 1936 there were 24 large plants and 537 small ones. By 1940 the survivors of these had coalesced into large, rather solid areas that subsequently began to break into segments. New plants again became established, and in 1946 there were 25 medium-sized and 265 small plants. These gradually died out, and in 1953 only 9 small plants were charted.

Between 1932 and 1936, when total basal area approximately doubled, the value of the loop-density index increased more than six times (Fig. 6). When the basal area again doubled between 1936 and 1940, the loop-density index decreased by about 30%. From 1943 to 1946 basal area decreased by 74%, but loop-density index decreased only 32%. The bias, or ratio between actual percent basal area and loop-density index, varied from 1.6, when most plants were large, to 12.5 when they were small.

Double hits, which included two or more plants, occurred in half the years. Therefore, the loop-density index was adjusted so as to equal the sum of all plants hit divided by the total number of ¾-inch plots. Estimates of basal area were then computed by equation (7) for each year using adjusted loop-density index and number of plants per unit area. These adjustments are only approximate because variability of plant size and shape were ignored in the computation. Year-to-year fluctuations of actual and computed basal areas shown in Fig. 6 vary in the same direction and maintain an approximately parallel relation. In all years except 1953 the computed percent basal area was less than the actual. Differences between actual percent plant area and the computed values are attributable mainly to the variety of plant sizes present in any one year, and also, to some degree, to sampling error.

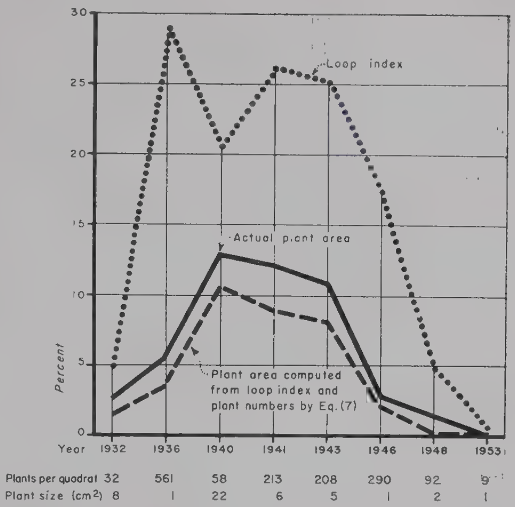


FIG. 6. Loop-density index and actual plant area in percent compared with percent plant area obtained by adjusting loop index for number of plants per unit area and spatial arrangement of plants.

DISCUSSION

In the loop-frequency method, where presence of a plant (or plants) is recorded irrespective of the portion of its area within the plot, the relation of frequency, or index, to percent plant area depends upon certain other attributes of the vegetation. Both percent plant area and index depend upon size and number of individual plants; but in addition, with constant plot size, the index is affected by plant shape, variability of plant size, and the pattern of plant distribution.

For a specific percent plant area many combinations of number and size of plants are possible; and for each combination of these inversely related variables there is a different loop-density index, even when plant shapes, etc., are ignored.

Differences in bias of the index, either from site to site or from one date to another on a specific site, can be more pronounced than differences in percent plant area, or vice versa. As has been shown above, the differences may even be converse. For many species it is only when actual differences in percent of area occupied by plants are rather great that similar differences can be expected in loop-density indices.

Comparisons (published and unpublished) made by other workers have shown loop-density indices to be correlated positively with percent plant area. In our tests this was true for the winterfat stands in which plant sizes were approximately equal, but not where plant size varied between stands. For the latter, differences in plant area were not consistently reflected by differences in loop-density index.

In sampling vegetation to determine plant cover by the loop method, it is necessary to be aware of its limitations. Most important to remember is that the index is not a direct measure of percent plant area. Before it can be construed to be such an estimate, it must be converted by using additional information obtained from the same plant population—dimension or number of individual plants. The conversion must still be considered only approximate because of the uncorrectable effect of plant shape on the bias. Recognition must also be given the fact that a great many hits are necessary for statistical reliability, especially on populations of small or scattered plants.

The influence of plant distribution or spacing on loop-density index can be eliminated by a change in the method of recording observations: by recording number of plants or parts of plants found in each plot rather than mere presence. The index derived from such data would no longer be an expression of plant frequency, but its conversion would result in closer approximation of percent plant area. We suggest, therefore, that this modification be adopted by users of the method.

The growth habit of certain species is such that no correction is needed for comparison of indices of the same species from different sites or from permanent plots observed on different dates. For species that vary little in individual plant area with time or from place to place—for example, single-stem rhizomatous grasses and broad-leaved herbs—differences in index are directly proportional to differences in percent plant area. Variations in plant area in such cases are due to variation in plant numbers. Since the relation between loop-density index and percent plant area is linear for plants of a given size (Fig. 3), no correction is needed before making the comparisons.

Likewise, where plants all have diameters about 6 or more times greater than the plot diameter, correction of the index is probably not necessary since the bias varies little with relatively large variations in percent plant area.

It is with species whose populations are made up of smaller individuals of various sizes, or which vary in average size from time to time or place to place, that correction of index is most necessary for interpretation. Either plant radius or number of plants per unit of area must be determined for use in calculating an estimate of percent plant area. More precision can be attained by using radius (Equation (8)) because sampling error is less exaggerated in conversion with this factor as a variable than where plant numbers are used (Equation (7)). However, with some plant populations, where it is obviously much easier to get an estimate of numbers than of plant radius, it may be desirable to sacrifice some precision of conversion for expediency. Numbers, rather than radii, were used to convert the indices from the mountain brome quadrat with reasonably satisfactory results. It should be pointed out, however, that about 10 percent of the area of the quadrat fell within the loop plots and that time seldom permits such intensive sampling in the field.

Indices of the winterfat stands were converted on the basis of plant numbers, but estimates of plant area by this method were not precise enough to reasonably approximate most of the plant area percentages derived from counts and measurement on 10-square-foot plots. The ratios of percent plant area determined by the latter method to percent plant area determined by correcting indices varied from 0.65 to 1.34. Although these two estimates were made from different data, and each had its own sampling error, it is probable that variability of plant size and irregularity of shape caused some of the discrepancy.

Size and number of plants are often difficult to determine with a satisfactory degree of precision. For interpreting the loop-density index, plant shape presents an even more formidable problem. The authors believe that for precise determination of percent plant area, the loop method is rather limited in usefulness of application. Although the element of personal bias is greater, small plots rated as to the percent of each occupied by plant area would probably give a much closer estimate of the true percent plant area than converted loop-density indices where plant shape, variability of size, and irregular distribution of plants complicate index interpretation.

SUMMARY

The inherent positive bias of the loop-frequency index as an index of percent plant area depends on plot (*loop*) *size,* and on *number* and *size of plants.* Algebraic equations by which loop indices may be converted to percent plant area are given. The influence of plant *distribution pattern* on the bias is shown, and a way to eliminate this effect, which cannot be corrected for by mathematical manipulation, is suggested. Deviation of *shape* of individual plants from circularity increases the bias, but no formula is available for correcting for this effect.

Some of the theoretical relationships were tested on synthetic and natural populations of plants. Results conformed closely to theory.

Possible modifications for reducing the inherent bias of the loop-frequency method are discussed.

REFERENCES

Aberdeen, J. E. C. 1958. The effect of quadrat size, plant size, and plant distribution on frequency estimates in plant ecology. Austral. Jour. Bot. **6:** 47-58.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Jour. Forestry **39:** 388-394.

Curtis, J. T. and R. P. McIntosh. 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology **31:** 434-455.

Goodall, D. W. 1952. Some considerations in the use of point quadrats for the analysis of vegetation. Austral. Jour. Sci. Res., Ser. B. **5:** 1-41.

Johnston, A. 1957. A comparison of the line interception, vertical point quadrat, and loop methods as used in measuring basal area of grassland vegetation. Canad. Jour. Plant Sci. **37:** 34-42.

Levy, E. B. and E. A. Madden. 1933. The point method of pasture analysis. N. Zeal. Jour. Agr. **46:** 267-279.

Parker, K. W. 1950. Report on 3-step method for measuring condition and trend of forest ranges. U. S. Forest Service, Washington, D. C., 68 pp. (Processed)

———. 1951. A method for measuring trend in range condition on national forest ranges. U. S. Forest Service, Washington, D. C., 26 pp. (Processed)

Sharp, L. A. 1954. Evaluation of the loop procedure of the 3-step method in the salt-desert shrub type of southern Idaho. Jour. Range Management **7:** 83-88.

Short, L. R. 1953. New equipment for the 3-step method. Jour. Range Management **6:** 184-186.

Winkworth, R. E. 1955. The use of point quadrats for the analysis of heathland. Austral. Jour. Bot. **3:** 68-81.

THE OCCURRENCE OF NATURAL ROOT GRAFTING IN EASTERN WHITE PINE, *PINUS STROBUS* L., AND ITS ECOLOGICAL IMPLICATIONS[1]

F. H. BORMANN AND BEN F. GRAHAM, JR.
Botany Department, Dartmouth College, Hanover, New Hampshire

INTRODUCTION

The concept of rooted green plants as discrete physiologic units is widely accepted among ecologists and is the basis for the strong emphasis placed on competition as a major force in vegetation dynamics. Yet there is considerable evidence, in the numerous reports of intraspecific root grafting (Bormann and Graham 1957, Graham 1959), that in many woody species two or more "individuals" may be morphologically interconnected. The question arises: does intraspecific root grafting sometimes connote a loss of individuality and introduce the possibility of intraspecific co-operation and/or parasitism in species subject to this phenomenon?

As a first approach to this fundamental question it was decided to investigate a single experimental organism. Eastern white pine, *Pinus strobus* L., a vigorous and widespread successional species, was chosen because of characteristics thought desirable to a study of this type. Its ability to form root grafts was demonstrated by LaRue (1934) who reported self grafts (between two or more roots of an individual tree) to be common, and intraspecific grafts (between two individuals of the same species) to occur. In northern New England, white pine frequently occurs in more or less dense, pure stands where the possibilities of root grafting are enhanced. Also, stands of all ages, growing under a wide range of environmental conditions, are accessible.

The objectives of the study were to develop techniques for the detection of root grafts, to determine the extent of root grafting in stands of various ages and in stands growing on various

---

[1] This work was supported by National Science Foundation Grant 3222, Atomic Energy Commission Contract AT(30-1)-2037, and the Cramer Foundation of Dartmouth College.

sites, and to learn whether grafts, thus detected, are functional in the translocation of substances between "individuals." It was hoped that these findings would form the basis for a more intensive study of the ecology and physiology of root grafts.

METHODS AND RESULTS

General Technique

To study the occurrence of grafting, it was decided to choose a number of variously aged trees growing under various site conditions and determine the degree to which each was grafted to its neighbors. Rather than use the cumbersome and time-consuming method of excavation to detect grafts, it was decided to inject each tree (hereinafter referred to as the donor) with a tracer substance and then detect, if possible, the tracer in adjacent trees. This technique has the advantage of a relatively small time investment, and it also demonstrates that grafts thus detected are functional in the translocation of materials.

Injection Technique

Certain investigators have taken pains to exclude air from their injection systems (Shevyrev 1894, Fraser and Mawson 1953, Greenidge 1955a and 1955b) while other workers (Roth 1896, Dickson and Blackman 1938, Morris 1951, and Graham 1954) have made successful injections without excluding air during the initial phase of the injection process.

To compare injection with and without exposing the xylem to air, the trunks of 4 trees, each approximately 8 m high, were bored to a depth of 5 cm at a height of 0.6 m above the ground level. In two, the hole was made with air admitted; and a tube leading from a reservoir of 0.15% aqueous acid fuchsin dye was stoppered into it. Residual air was bled from the hole by means of a syringe. In the remaining trees the hole was bored beneath the surface of the dye held in a v-shaped cup. Dye was maintained at a constant level by a gravity feed system from a one-gallon reservoir.

After several days, the trees were felled and sectioned at 0.5 m intervals. The pattern in the sapwood indicated that dye injected without exposing the xylem to air travelled throughout the system more rapidly, while dye injected in air moved more slowly although it seemed that it would ultimately travel as far. Admitted air, apparently, slows the initial rate of intake of injected materials—a conclusion reached by other workers in this field (Stoddard and Dimond 1949).

In all instances it was noted that the dye moved upward in a relatively narrow streak exhibiting little tangential spread within the sapwood (Fig. 1). Similar results were obtained by Fraser and Mawson (1953) using radioactive Ca in white pine, and by Mirov (Thimann 1958, p. 39) using various substances in ponderosa pine, *Pinus ponderosa* Laws. The ascending dye streaks tended to form a spiral pattern in the sapwood—usually dextrally oriented (Figs. 1, 2). This pattern may have been due to spiral grain as suggested by Morris (1951) and Fraser and Mawson (1953) in their discussions of spiral movements observed in white birch, *Betula papyrifera* Marsh., and yellow birch, *B. lutea* Michx. f. Since no anatomical investigation was made in this instance, however, no conclusion can be drawn.

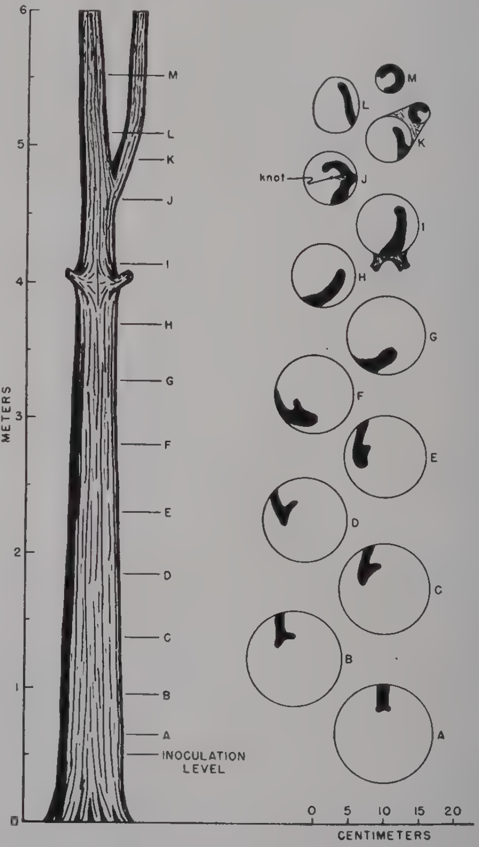


FIG. 1. Diagram of the dye pattern in a white pine tree resulting from a single hole injection with air excluded. The dye is shown as it appeared in cross sections made at the heights indicated.

A seemingly consistent difference was observed in dye patterns formed as a result of injection with and without exposing the xylem to air. With air admitted, dye moved upward in the inner layers of the sapwood, whereas with air excluded, dye ascended in both inner and outer sapwood (Fig. 2). Similar results have been obtained with various hardwoods. In white birch, dye transfer, resulting from single injections in air, seems confined to the deep sapwood (Morris 1951), while illustrations in Greenidge (1955a) indicate that underwater injections into other hardwoods usually result in transfer in the outermost sapwood. This suggests a difference in the mechanics of transfer in inner and outer sapwood.

To obtain information on movement of dye up and down the trunk, each of 8 trees in a 27-year old plantation was injected with 0.15% aqueous acid fuchsin through a single hole 7.5 cm deep and 1.5 cm in diameter bored 1 m above the ground level. Four trees, numbers 2, 3, 7, and 8, were girdled by deep ax cuts approximately 0.5 m above the injection site, while trees 4, 5, 6, and 9 remained ungirdled. In trees 2, 3, 5, and 6 air was excluded during injection, while in trees 4, 7, 8, and 9 air was admitted.

After one week, the 8 trees were felled, the trunks were sectioned, and the crowns and roots were examined for the presence of dye. The results are summarized in Table I, and the dye patterns occurring in the trunks are shown in Fig. 2.

TABLE I. Distribution of dye in trunks, crowns and roots of white pine trees. Dye was injected with air admitted to or excluded from the injection site. Trees were not girdled or were girdled above the injection site. The presence of dye is indicated (+), its absence (−)

	TREES GIRDLED				TREES NOT GIRDLED			
	Air admitted		Air excluded		Air admitted		Air excluded	
Tree no.	7	8	2	3	4	9	5	6
Trunk*	−	−	−	+	+	+	+	+
Crown	−	−	−	+	−	−	+	+
Roots	+	−	+	+	−	−	−	−

* =above the girdle.

Dye moved upward through the trunks in all non-girdled trees, while it failed to move past 3 of the 4 girdles. In tree number 3, dye was visible above and below the girdle, indicating translocation through deeper sapwood. Dye was found in the crowns of trees 3, 5, and 6, while, perhaps due to the retarding influence of air, it was absent in trees 4 and 9. In view of the anticipated root transfer studies, the effect of girdling on downward movement was significant. Dye was found in the roots of 3 out of 4 girdled trees but in none of the roots on non-girdled trees.

The above considerations suggested that a technique for injecting tracers to be translocated between grafted white pine trees should: 1) eliminate typical upward movement in the injected tree to allow movement of the tracer into the roots; 2) expose to tracer intake as much of the vascular system as possible, thus minimizing the streak effect typical of single hole injections, and allowing all roots of the injected tree equal access to the dye; and 3) make injections under water to speed translocation of the tracer.

A technique was developed in which the donor tree was felled, a collar built around the stump, and the tracer substance placed in the collar. The collar technique met the first two requirements mentioned above, but not the third. It was felt, however, that the advantages of speedier installation, complete exposure of the xylem to the tracer, and ease of measurement of rate of intake would offset any disadvantage occasioned by admitted air.

To construct a collar, the experimental tree was felled with a chainsaw and, when necessary, the bark around the top 10 cm was smoothed with a machete. The stump was ringed with a strip of caulking compound (Vulcatex, A. C. Horn Company), and a strip of strong building paper (Sisalation, American Sisalcraft Corp.), wide enough to cover the caulked area and extend 20 to 30 cm above the stump surface, was pulled tightly around the stump and stapled. The joint of the collar was then caulked and stapled and all edges were covered with an additional one-in. strip of Sisalation and recaulked with Vulcatex. A cylinder of quarter-in-mesh hardware cloth was placed within the collar to provide rigidity (Fig. 3). To exclude rain, animals, and debris and to prevent evaporation, a polyethylene cover, held up by a large spike driven into the heartwood, was stretched over the collar and held in place with a rubber band (Fig. 3). A small ruler attached to the central spike facilitated measurement of changes of solution level within the collar. Collars of this design were usable for as long as 4 months. A similar arrangement has been used by True, *et al.* (1955).

To check the efficiency of this method of injection, Graham (1959) sectioned injected stumps 10 cm below the collar. He found that the whole sapwood, except in cases where portions of it appeared to be diseased or non-functional, was deeply stained with acid fuchsin, while the heartwood showed no evidence of dye (Fig. 4). Additional data on dye movement were obtained when a stump from Stand 4 (Fig. 5) was excavated 6 weeks after injection. Ten months later, after

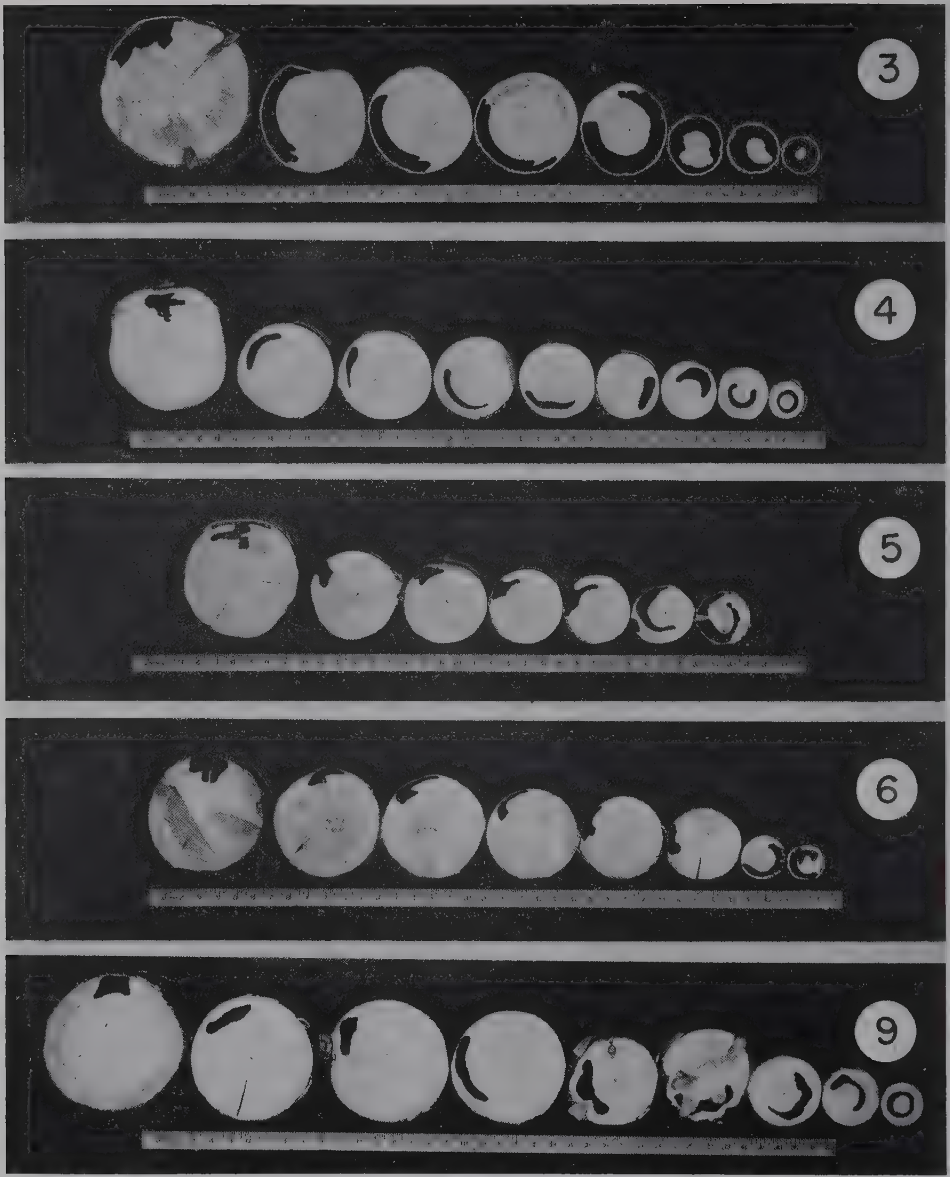


FIG. 2. Dye patterns (inked) resulting from injections made without exposing the xylem to air, trees 3, 5, and 6, and those made after exposing the xylem to air, trees 4 and 9. The sections were made at approximately 1.2 m intervals, and are arranged in ascending order from left to right. All sections have the same orientation as the one at the left.

storage outdoors, the stump was sectioned 30 cm below the collar, and all major roots were sectioned approximately 50 cm from the stump axis (Fig. 5). The dye colored a continuous ring of outer sapwood in the trunk, and streaks of dye were evident in the sapwood of many of the roots, despite the fact that only one root was found to be grafted to a neighboring tree. The phenomenon of dye moving into ungrafted roots was also observed in other donor trees. Apparently, some-

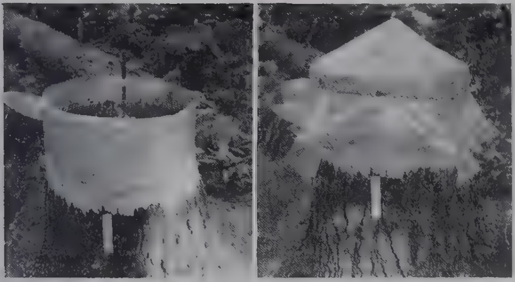


FIG. 3. *Left.* Collar for retaining tracer solution on the cut surface of a donor stump. *Right.* Polyethylene cover in place.

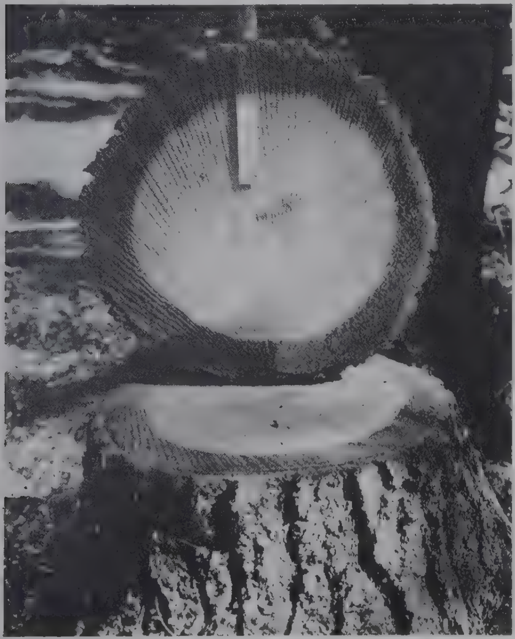


FIG. 4. A section made 10 cm below the cut surface of a donor stump showing heavily dyed sapwood.

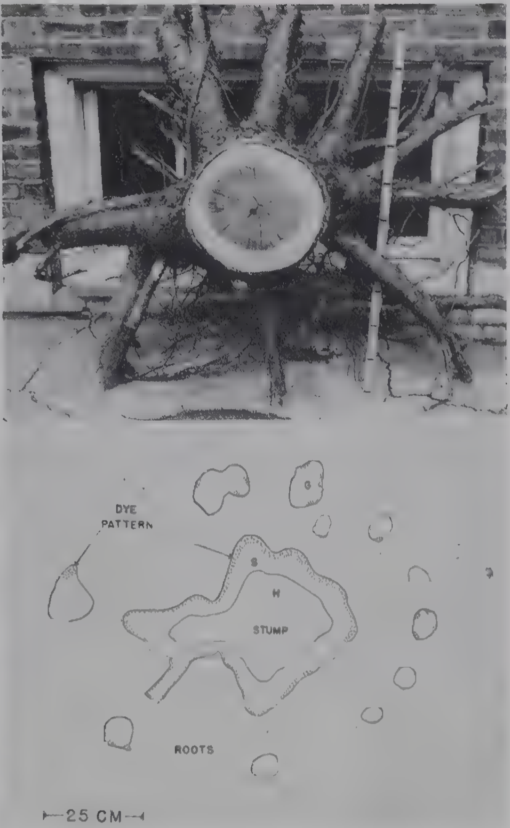


FIG. 5. *Top.* Donor stump 4-10 showing the spreading and shallow habit of the major roots. A few small roots composed the deep root system. *Bottom.* Stump 4-10. Dye pattern shown as stippled areas in a cross-section of the stump made 30 cm below the injection surface and in root sections made 50 cm from the vertical stump axis. Heartwood, sapwood, and the only root found to be grafted to a receptor tree, are indicated H, S, and G, respectively.

thing more than "transpiration pull" through root grafts operates to cause dye to move into the roots.

Tracer Substances and Detection Methods

Solutions of dye and radioisotopes were used as tracer substances. A 0.15% solution of aqueous acid fuschsin was selected because of its previous successful use by other workers (Morris 1951, Greenidge 1955a), and its modest cost.

It was originally planned to detect dye in receptor trees by removing small cores with a Swedish increment hammer. Dye transferred from donor to receptor trees, however, moved upward in streaks, the size and position of which were determined by the nature of the graft union. Dye moving through small roots or young grafts ascended in narrow streaks which often escaped detection with the increment hammer.

The method finally adopted involved lifting flaps of bark on the horizontal roots near the base of each potential receptor tree to expose any streaks of dye. In this way dye was detected which increment punches had failed to reveal.

The radioisotopes Rubidium-86 and Iodine-131 were used as tracers because: 1) both have been used successfully in injection experiments (Fraser and Mawson 1953, Kuntz and Riker (1956); 2) both are strong gamma emitters and are thus detectable through a certain amount of soil or wood; and 3) both decay fast enough to minimize the hazard incident to their use under field conditions (half-lives are Rb-86, 19.5 days; I-131, 8.1 days).

Rb-86 in the form of RbCl was placed in the collars in a carrying solution of 1% KCL following the method of Fraser and Mawson (1953), while I-131, in the form of NaI, was used with a carrier of 1% $NaSO_4$ plus 1% NaI.

Radioactivity was detected with a portable scintillator (Model 111B, Precision Radiation Instruments Inc.). A 3 mm cylinder of lead was placed over the probe containing the sensitive sodium iodide crystal, thus improving the directional sensitivity of the instrument.

To obtain an estimate of the comparative efficiences of tracers, dye and Rb-86 were injected into 5 donor trees, and dye and I-131 were injected into 4 donor trees (see section on Stand 4 for details). In the latter instance, no transfer of dye or I-131 occurred. This negative result will be discussed in a later section. In Stand 4 where dye and Rb-86 were used, 4 of the 5 donor trees were found to be grafted to a total of 5 receptor trees. In 4 of the 5 receptors, dye and Rb-86 were easily detected. In the fifth receptor, however, a small graft of 5.5 m from the donor was detected through radioactivity (Fig. 6), while dye, barely visible at this graft, probably would have gone unnoticed. It was concluded, therefore, that dye is probably as efficient as Rb-86 in the detection of major grafts, but is less efficient in the detection of minor grafts.

In summary, advantages were found for both acid fuchsin and Rb-86 as tracers in locating root grafts. Acid fuschsin is inexpensive, presents no special handling problems, allows visual study of the translocation pattern, involves no health hazard and, consequently, may be used on any site. Its use probably results in the detection of most grafts that can be detected by injection. However, when much diluted in the sapstream, and when distributed in narrow ascending streaks, it may be overlooked. Further, its detection necessitates injury to the receptor trees. By comparison, Rb-86 is expensive, requires care and some specialized equipment in its handling, and presents a temporary hazard at the inoculation site. The hazard, and the stipulations of the isotope license, limit to a considerable extent the experimental areas in which radioactive materials may be used. Advantages are that the Rb-86 can be readily detected even when very dilute, and its detection requires no injury to receptor trees.

Experimental Stands

During the summer of 1957, 81 experimental plots were established in 5 white pine stands. Stands were selected to represent different age classes and various site conditions. Soil underlying each stand was examined and samples from each horizon were collected and later subjected to mechanical analysis.

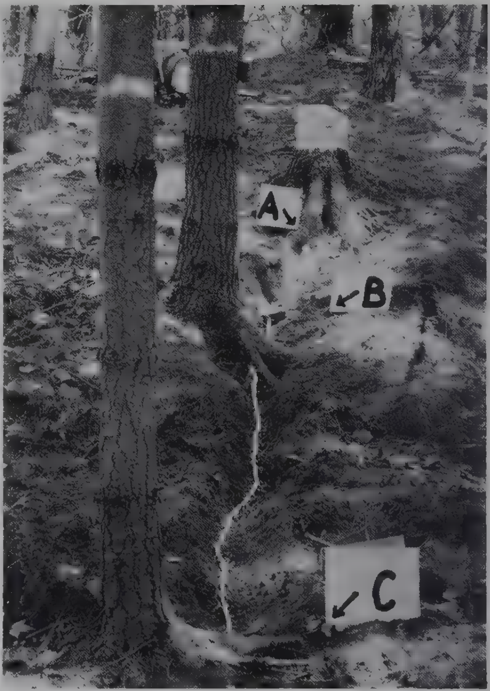


Fig. 6. Plot 4-10, showing the root (painted white) through which Rb-86 and dilute acid fuchsin were transported 5.5 m to a receptor tree. The origin of the root at the donor stump is indicated by (A), while (B) indicates a false graft, and (C) marks the site of the true graft.

Each plot was composed of a central donor and its adjacent potential receptor trees. Trees selected for donors were healthy but not necessarily dominant. Individual plots were separated by distances thought sufficient to eliminate the possibility of a tracer being translocated from a donor on one plot to a receptor on another plot.

The height, age, DBH, height to lowest live branch, vigor, and the radius of sapwood and heartwood were recorded for each donor, while DBH, distance to donor, and azimuth from the donor were recorded for each potential receptor.

Stand 1.—The youngest stand used was a 15-year old natural pine stand occurring on a 27% northwest facing slope in Lyme, New Hampshire. Underlying this stand was a loamy sand, about 45 cm deep, which rested on a blue-gray, mottled, brown silt loam subsoil. These soil and slope conditions indicated excellent drainage on the surface and in the upper soil, but slow drainage in the deeper soil. The stand, densely stocked, had an average of 117 trees per 100 squares meters of experimental plot. The average DBH of trees on the experimental plots was 6.6 cm.

On August 6, 1957, 20 experimental plots were established. Acid fuchsin was placed in the collars and maintained at a depth of 1 to 4 cm for about 3 weeks. All trees within 1.5 m of the donor were considered as potential receptors and were examined several times, the last examination occurring November 10.

The results, presented in Table II, indicate that 10 of the 20 donor trees transferred dye to 11 receptor trees. The data also indicate that donor trees are most likely to be grafted to their nearest neighbor.

TABLE II. Data on dye transfer through root grafts in Stand 1, a 15-year old natural stand

Donor Tree dbh in cm	Receptor Trees		Nearest Non-receptor Tree	
	Distance from Donor m	dbh in cm	Distance from Donor m	dbh in cm
5......			0.4	4
5......	0.1	6	1.5	7
5......	0.3	5	0.1	3
—	0.3	3	—	—
6......			0.3	8
7......			0.2	3
7......			0.4	9
5......			0.3	3
5......	0.2	8	0.1	7
5......	0.3	3	0.3	2
6......			0.6	6
6......	0.6	6	0.5	6
10......			0.2	11
5......			0.6	7
9......	1.5	6	0.8	5
6......			0.5	9
11......			0.8	16
7......	0.4	7	0.3	3
6......	0.3	5	0.3	6
10......	0.3	6	0.4	9
9......	0.3	9	0.3	8
Av. 6.8....	0.4	5.8	0.4	6.6

Stand 2.—The second stand was a 19-year-old naturally occurring stand growing on a 13% northeast slope in Hanover, New Hampshire. The upper soil under this stand varied from loam to sandy loam and was about 25 cm deep. Beneath this was a sandy loam subsoil, from 15 to 50 cm deep, containing scattered pebbles. On this site both surface and internal drainage appeared to be excellent. The density of the stand on the experimental plots was 69 stems per 100 square meters. The DBH averaged 7.6 cm.

On June 19-20, 20 experimental plots were established. Acid fuschsin was maintained in the collars for about 5 weeks. All trees within 1.8 m of the donor were considered as potential receptors. The last examination was made on October 17.

The results, presented in Table III, indicate that 6 out of 20 donors were grafted to a total of 7 receptor trees. Again, the nearest neighbor tended to be the grafted tree, but 2 receptors were more than twice the distance to the nearest non-grafted tree.

TABLE III. Data on dye transfer through root grafts in Stand 2, a 19-year-old natural stand

Donor Tree dbh in cm	Receptor Trees		Nearest Non-receptor Tree	
	Distance from Donor m	dbh in cm	Distance from Donor m	dbh in cm
10......			0.7	4
11......	1.4	5	0.4	8
8......			0.5	4
11......			0.8	5
10......			0.6	9
8......	0.4	6	1.0	8
8......	0.2	5	0.4	5
—	0.5	6	—	—
12......	0.2	3	0.5	11
12......			0.8	10
12......			0.4	6
8......			0.4	10
12......			1.2	10
12......			0.8	7
12......			0.7	12
12......	0.6	9	0.7	4
13......			0.7	11
13......			0.5	7
12......			0.9	7
8......			0.7	8
8......	1.2	16	0.6	8
Av. 10.6....	0.6	7.1	0.7	7.7

Stand 3.—The third stand was a *27*-year old pine plantation on relatively level ground beside the Hanover, New Hampshire, reservoir. The upper 40 to 50 cm of soil, a sandy loam with cobble-sized stones, was underlain by a gray, pebbly sandpan with light brown mottling. Surface drainage was estimated to be fair, while internal drainage was rated as poor. The trees, planted on a 6 x 6 ft. spacing, had not been thinned, but underbrush had been cleared regularly. Density per 100 square meters of experimental plot was 30, and average DBH was 16.2 cm.

Four plots were installed on June 6, and an additional 16 plots were started on June 13-14. Acid fuchsin was maintained in the collars through the end of June. All trees within 4.6 m of the donor were examined for the presence of dye several times throughout June and July.

Results presented in Table IV show that 10 out of 20 donors transferred dye to 14 receptors. The average distance to the receptors, 1.6 m, reflects the 6-ft. spacing of the plantation.

TABLE IV. Data on dye transfer through root grafts in Stand 3, a 27-year-old plantation

	RECEPTOR TREES		NEAREST NON-RECEPTOR TREE	
Donor Tree dbh in cm	Distance from Donor m	dbh in cm	Distance from Donor m	dbh in cm
21......	1.6	20	1.7	15
—	2.4	16	—	—
14......	1.6	15	1.7	15
18......			1.7	21
18......			1.8	9
15......			1.8	10
20......			1.8	20
15......			1.6	20
16......	0.9	13	1.5	23
24......	0.6	17	2.1	15
26......	4.3	6	1.5	18
—	1.2	14	—	—
21......			2.1	12
21......			1.4	12
16......			0.8	15
16......	0.6	15	2.1	21
20......			2.0	22
20......	1.5	13	2.0	15
15......	1.0	12	1.3	15
12......	1.7	25	1.9	13
24......	2.0	19	2.0	12
—	2.7	21	—	—
—	2.0	16	—	—
18......			1.1	20
Av. 18.6....	1.7	15.9	1.7	16.2

Stand 4.—Through the co-operation of the Vermont Forest Service, plots were established in a 39-year-old plantation in the Downer State Forest Annex near Sharon, Vermont. This stand occurred on an east-facing exposure with slope up to 30%. Ten to 20 cm of sandy loam to loamy sand rested on 50 to 100 cm of sandy subsoil which graded into rotted schist below. Overall drainage was excellent. Average density per 100 square meters of plot was 16, and DBH averaged 19.8 cm.

Nine plots were established on July 5 and 6. On 5 plots, 10 millicuries of Rb-86 and its carrier were placed in the collars. Three hours later, after the isotope solution had been absorbed by the stumps, acid fuchsin was placed in the collars. On the 4 remaining plots, 10 millicuries (20 mc for tree 1-3) of I-131 plus its carrier and acid fuchsin were placed in the collars. Dye was subsequently maintained in all the collars for approximately one week. On both sets of plots, all potential receptor trees within 4.6 m were monitored for radioactivity and examined for dye 6 times during the 19-day period following injection.

Results from Stand 4 are presented in Table V. Six days after inoculation, 3 donors had transferred Rb-86 and dye to single receptors. Five days later, a fourth donor was found to have transferred tracers to a single receptor, and a second receptor was found for one of the earlier donors.

TABLE V. Data on dye and radioisotope transfer through root grafts in Stand 4, a 39-year-old plantation

	RECEPTOR TREES		NEAREST NON-RECEPTOR TREE	
Donor Tree dbh in cm	Distance from Donor m	dbh in cm	Distance from Donor m	dbh in cm
	RUBIDIUM-86			
28......	1.8	16	1.7	19
24......	1.6	26	1.7	26
18......	2.2	25	1.8	20
—	2.0	24	—	—
18......			1.9	28
25......	5.5	15	2.1	18
	IODINE-131			
24......			1.9	19
24......			2.4	21
28......			1.5	17
26......			1.8	15
Av. 23.8....	2.6	21	1.9	20.3

Four out of 5 donors were found to be connected to 5 receptors. Although 3 of the 4 were grafted to nearby trees, one had a root that extended for 5.5 m where, with a diameter 1.3 cm, it was grafted to a large root of a 14.7 cm tree (Fig. 6).

Neither radioactivity nor dye was detected in any receptors on the I-131 plots. Both tracers moved into donor stumps but only for short distances. The selection of 4 ungrafted donors here, when 4 out of 5 Rb-86 donors were grafted, seems statistically improbable, and the possibility that the combination of I-131, 1% $NaSO_4$, 1% NaI, and dye was not a suitable tracer seems likely.

It is noteworthy that 22 of 26 stumps of white pine trees, thinned from this stand at about the time of the I-131 injections, were living one year later, while all of the I-131 stumps were dead. Page (1927) suggests that living stumps following thinning are an indication of root grafting. In 2 thinned stands, 53- and 88-years-old, he found 58 and 54% of the stumps of thinned trees alive after one year. Limited excavation revealed that living stumps were invariably grafted to neighboring trees. Data from the Rb-86 plots support this conclusion. Of the 4 inoculated stumps known to be grafted, all were alive one year later and most of the new living tissue was located over roots which were grafted to receptor trees. The single Rb-86 stump for which no receptors had been found was dead. Assuming that 85% of the trees thinned from the area surrounding the I-131 plots were grafted to living trees, the failure of any of the I-131 trees to show connections with adjacent trees, for whatever cause, gives an erroneous picture of the amount of grafting in this stand.

Stand 5.—This uneven-aged pine stand, in Hanover, New Hampshire, occurred on a northwest exposure with a slope of approximately 10%. The site was underlain by approximately 50 cm of sandy loam which graded into 50 cm of tight, yellow-gray subsoil. The subsoil, in turn, graded into weathered mica schist. Surface drainage was good, but subsurface drainage appeared to be poor. The stand was composed of large pines with a low understory dominated by white ash, *Fraxinus americana* L. Pine density per 100 square meters of experimental plot was 4.4.

Ten plots, with donors varying in age from 30 to 72 years, were established on July 15-16. Acid fuchsin was used as a tracer and was maintained in the collars for approximately 3 weeks. Two additional plots were established on August 3, when 15 mc of Rb-86 were injected into 2 donor trees. All trees within 6.1 m of the donor trees were examined for tracers.

Rate of dye intake by donors, diurnal fluctuations in dye intake, effect of weather on intake, and other relationships of grafting were studied by Graham (1959).

Results presented in Table VI indicate that 8 of 12 donors were grafted to 14 receptors. Eight of the 14 receptors were more than 0.5 m farther from the donor than was the nearest non-grafted tree.

TABLE VI. Data on dye or radioisotope transfer through root grafts in Stand 5, an uneven-aged natural stand. Donor trees ranged from 30 to 72 years of age, averaging 55 years

	RECEPTOR TREES		NEAREST NON-RECEPTOR TREE	
Donor Tree dbh in cm	Distance from Donor m	dbh in cm	Distance from Donor m	dbh in cm
31	2.7	44	2.1	29
—	3.2	44	—	—
25	0.8	19	3.1	24
—	1.8	28	—	—
23			1.4	24
19	1.2	30	1.1	20
—	1.6	25	—	—
26			0.5	21
32	3.4	52	3.4	15
—	3.9	56	—	—
24	2.6	40	0.9	32
18	2.8	47	2.0	6
—	3.8	47	—	—
35			2.4	41
47	3.4	42	3.5	41
—	4.3	40	—	—
30*	1.8	**	**	**
28*			**	**
Av. 27.7	2.7	39.5	2.0	25.3

* Radioactivity used.
** No data.

Grafting in a Bog Forest

An unusual opportunity to study root grafting in a white pine bog forest was afforded with the discovery of an exposed root network in Georges Pond Bog in Enfield, New Hampshire. Years ago the outlet to this bog was dammed and the roots of a forest stand growing in peat were submerged. Ultimately the tops of the trees broke off or were sawed off, but the stumps and the roots remained in place. Approximately 20 years ago, the dam was broken, the water level receded, and a root network of 6 trees was almost wholly exposed on the surface of the partially drained peat. Using a 0.5 m string grid, a sketch of the network was made on graph paper. Also a sample of wood was removed for identification and a fallen trunk was bored to ascertain its age.

The wood was identified as white pine by Professor F. S. Page of Dartmouth College. The boring revealed that the trunk was at least 70 years of age. Thus it was concluded that this network represented a group of fairly old trees growing on a deep peat soil.

Figure 7 indicates the high degree of grafting that occurred among these 6 trees. Many self grafts and several intraspecific grafts are evident, despite the fact that parts of the network had been removed for firewood by hunters or fishermen.

Poisoned Stand

In the spring of 1958, Mr. T. W. McConkey of the U.S. Forest Service called the writers' attention to a 32-year old stand of white pine on the Massabesic Experimental Forest in southern Maine. The stand, planted in 1926 on a 6 x 6 ft. spacing, also contained some volunteer trees. It was thinned on August 31, 1956, by placing a tablespoon of ammonium sulphamate (ammate) crystals in one or two ax cuts made in unwanted trees. Soon after poisoning, injury and ultimately death of all treated trees and many non-treated trees was noted.

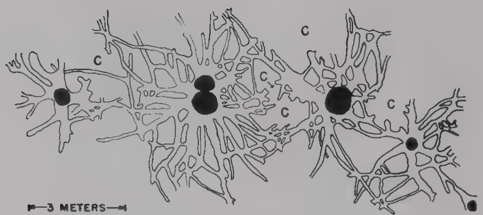


FIG. 7. Diagram of a root network exposed on the surface of a deep, partially drained peat soil. Black circles represent old stumps, and C's indicate areas where some roots have been removed by chopping.

During July 1958, the area was mapped and five 10 x 10 m plots, covering approximately 18% of the stand, were established throughout the plantation. On each plot the DBH of each treated tree and of each living, injured or dead non-treated tree was recorded, as was the distance from each non-treated tree to the nearest treated tree. Special care was taken to exclude trees known to be dead prior to the treatment. The soil under each plot was examined by means of a soil pit and/or several auger holes. Samples were removed from major horizons for mechanical analysis.

On all plots a total of 71 treated and 80 non-treated trees was recorded. Of the latter group, 33 trees were dead, 1 injured, and 46 were found to be alive and seemingly healthy. Thus 43% of the non-treated trees were dead or injured after approximately 2 years. Death or injury of the untreated trees may have been caused by poison leached into the soil from the implantation sites, or poison may have been translocated to non-treated trees through root grafts.

If leaching had been the cause, it seems that all trees should have sustained some injury, but dead and healthy trees occurred side by side. Numerous root grafts, revealed by excavation, indicated that the poison had been translocated from treated trees.

Removal of a 6-in. strip of bark from a tree with partial crown damage revealed a dark brown streak, due to ammate poisoning, in the outermost ring of sapwood (Fig. 8). The streak was traced down the trunk to a branch whorl, below which it was visible only as a faint discoloration in the innermost rings of sapwood. Ultimately the discoloration passed into a major root where it was no longer visible. Careful excavation, however, revealed that a branch root, 1.5 cm in diameter, was grafted to the face of a large root of a poisoned tree 2.3 m away (Fig. 9). Although the branch root was dead, the newest wood of the main root to which it was connected was alive, suggesting that ammate was carried in the deeper sapwood as was the case with the lower trunk. Excavation of 2 other dead non-treated trees revealed that one was grafted to a poisoned tree through 6 grafts ranging in diameter from 2 to 6 cm (Fig. 10), while the other was connected to a poisoned tree through 2 grafts 2 and 3 cm in diameter.

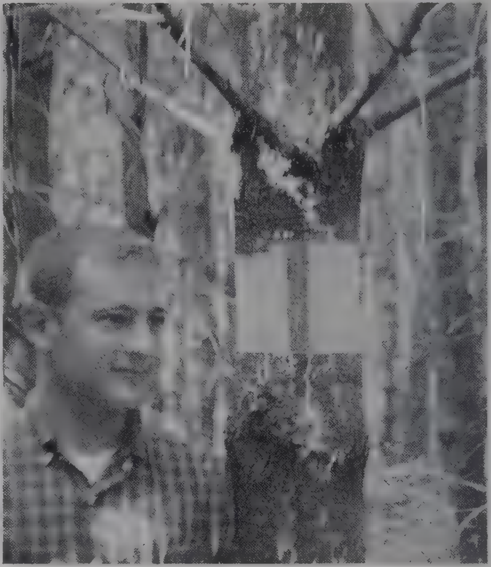


FIG. 8. Dead streak, in the outermost sapwood of a non-treated tree, resulting from the translocation of ammate through a natural root graft.

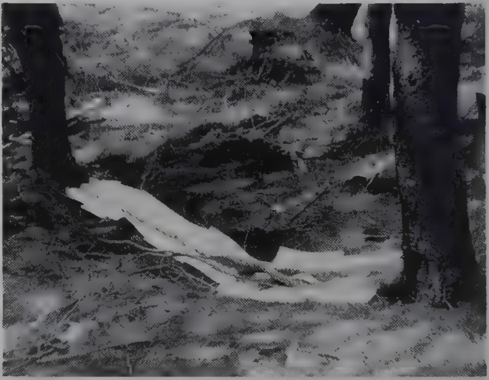


FIG. 9. The small root responsible for translocation of ammate from a poisoned tree (left) to a non-poisoned tree (right), causing damage shown in Fig. 8.

Soils were predominantly loamy sands with estimated drainage ranging from excessive to moderate. Although there were large plot to plot variations in the number of non-treated trees

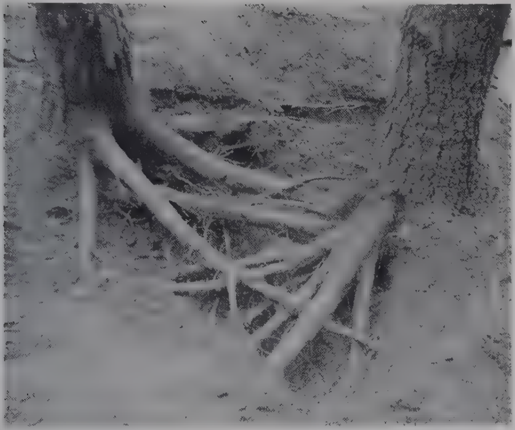


FIG. 10. The tree on the right was killed by ammate translocated through natural root grafts from the poisoned tree on the left.

killed, there was no obvious correlation between kill and soil conditions.

Living Root Systems on Old Stumps

During the study of Stand 5, it was noted that some old stumps and trees whose tops had been dead for a considerable time had living root systems. Injection experiments and excavation indicated that life in these systems was maintained with nourishment received from living trees through root grafts.

Four such seemingly dead trees were cut, the stumps collared, and 5 mc of Rb-86 with its carrier were poured into each collar. Within 70 hours, 3 of the 4 stumps had transferred Rb-86 to a nearby living tree. In the fourth stump, which failed to show transfer, it is probable that the radioactive solution ran into, or out through, a decayed area before a detectable quantity could be taken in by the narrow and discontinuous rings of live sapwood. The existence of grafts was further verified by the excavation of 4 stumps with live roots. All were found to be grafted to nearby living trees.

The occurrence of grafts between live trees and living roots of old stumps is common. A survey made on Stand 5 by cutting into roots near the base of seemingly dead stumps or trees indicated that 15 out of 23 had living root systems. Another survey, made in a 71-year-old stand occurring on deep sand in the Massabesic Experimental Forest in southern Maine, gave similar results. On a 20 x 20 m plot, 53 living trees, 13 standing dead tops, and 11 stumps in all stages of decay were counted. Seven of the 13 tops and 3 of the 11 stumps were found to have living roots—roughly 41%. Other cursory examinations of white pine stands of various ages indicated that living stumps were common. In old stands, some living stumps which have decayed to below ground level may escape detection. As a general rule, however, living roots are easily detected and their presence on seemingly dead stumps and trees provides a convenient indication of root grafts.

DISCUSSION

Intraspecific Grafting in White Pine

Natural root grafts, described many times in the literature, have been considered primarily as botanical curiosities; yet the union of 2 or more individuals through functional root grafts poses many fundamental physiological and ecological questions. To begin an exploration of these questions, white pine, a vigorous and widespread species, was chosen for study. Factors considered in making this choice were its occurrence in numerous more or less pure stands of all ages, and its growth under a wide range of environmental conditions.

An injection technique was developed whereby a tree was felled, a tracer substance was placed in a watertight collar built around the stump, and, subsequently, the surrounding trees were examined for the presence of the tracer. Thus intraspecific grafts were detected and, at the same time, their functionality was demonstrated. A total of 81 trees and 3 stumps in 5 stands, ranging in average age from 15 to 55 years and occurring under various soil and drainage conditions, were injected with 0.15% aqueous acid fuchsin and/or Rb-86 or I-131. The data are summarized in Table VII.

TABLE VII. Natural root grafts in white pine stands detected through the use of radioisotopes and dyes

Stand Number	Av. age of Stand	Density Stems per 100 m²	Average dbh cm	No. Donor Stumps	No. Donor Stumps Grafted	No. of Receptor Trees
1.......	15	117	7	20	10	11
1......	19	69	8	20	6	7
3......	27	30	16	20	10	14
4......	39	16	20	9	4	5
5......	55	4	31	12	8	14
5......	Stumps	4	31	3	3	3
			Total.....	84	41	54

Of the 84 trees and stumps injected, 41 were found to be grafted to 54 receptor trees. These findings are in accord with those of Page (1927) who found that 58 and 54% of the trees thinned from 53- and 58-year old white pine stands were grafted to living trees, and with those of Kuntz and Riker (1956), whose experimental work led them to conclude that intraspecific root grafting is frequent in white pine. The injection data are also in line with the observations on a 30-year-old stand, thinned by poisoning, where 43% of the residual stand died because of poison translocated through root grafts.

The data indicate that root grafting, involving from 30 to 67% of the injected trees, occurred on all sites. Although no conclusions can be drawn as to which site conditions are most conducive to the occurrence of grafting, it may be noted that root grafting in white pine occurs among trees growing in upland soils ranging from sandy loams to loams, in soils that are stony or free from stones, and under upland drainage conditions ranging from excellent to poor. The observations made at Massabesic Experimental Forest and at Georges Pond Bog show that considerable grafting may occur on extremely dry sites underlain by coarse, well-drained sands and on extremely wet sites underlain by bog peats. On all sites where grafts were unearthed, almost all occurred within the upper 12 to 18 in. of soil. Presumably this was due to the inherent shallow root system of the species (Fig. 5).

It is probable that given proper spacing conditions intraspecific root grafting will occur among white pine trees growing under the whole range of soil conditions tolerated by the species population. This further suggests that the occurrence of grafting is more or less independent of soil conditions, i.e., rocky soil, shallow soil, moist soil, etc., is not necessary.

For the most part, the development of grafts in white pine follows the pattern set forth for Scotch pine, *Pinus sylvestris* L., by Yli-Vakkuri (1953). Two roots, of the same or different size, grow parallel to each other or across each other establishing a point of contact. Since both roots are anchored in the soil, proximally and distally to the point of contact, subsequent radial growth causes a pressure to develop at the point of contact. Around the pressure point, growth appears to be stimulated and both roots often develop ridges of tissue; eventually the intervening bark is broken down and vascular continuity is established. Stimulation of growth may be due to the same factors that give rise to reaction wood in white pine shoots as discussed by Sinnott (1952). It has been suggested that wind action may cause roots to rub together and thus induce grafting (Cook and Welch 1957). This could help to break down the bark barrier between ridges, but it seems that such action would later disrupt the delicate processes of vascular organization at the cambial interface. Furthermore, in the healing over of living stumps, no rubbing action is necessary for the formation of a continuous cambium between the tissues advancing across the stump surface. Often after a graft is fully formed, a pocket of bark is isolated at the original point of contact within the graft. Similar pockets have been illustrated for other species (Franke 1883, Newins 1916, Neeff 1922, Rubtsov 1950).

Grafting was found in stands ranging in age from 71 to 15 years, and it probably occurs in relatively dense younger stands. Kuntz and Riker (1956) have reported root grafting between 4-year-old red pines, *Pinus resinosa* Ait., growing in nursery beds.

The detection of a receptor tree by injection indicates only that it is grafted to a donor and gives little information on the size and number of grafts between trees. Excavations of some trees revealed that grafts varied from 0.5 cm to 10 cm in diameter. Numbers of grafts ranged from one, between 2 trees, to 35, exposed through the partial excavation of 6 trees which were united through a complex root network. Excavation of roots near the bases of receptor trees on Stand 5 indicated that 31 roots transported dye to 13 receptor trees. Since dye in the proximal portion of a root often comes from more than one graft, it seems safe to assume that more than 31 individual grafts occurred. In fact, 35 direct or indirect (between a receptor and a second-order receptor) grafts were traced to a single donor in Stand 5. Other examples of the size and number of grafts are shown in Fig. 10, where 6 grafts between two 30-year-old trees are shown, and in Fig. 11, where massive grafting between two older trees is illustrated. Although some trees are linked together through a single small graft, it may be concluded that very

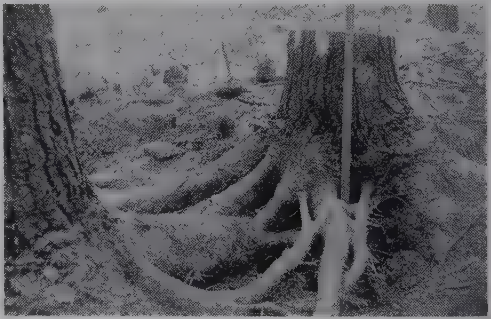


FIG. 11. Massive root grafting between a large tree and the stump of one cut the previous year. Photo by Professor F. S. Page.

often trees are linked together by sizable and numerous vascular connections.

In the authors' opinion, the injection data underrepresent the actual number of trees grafted to donor trees because: 1) some small, weak streaks and some streaks deep in the sapwood were probably missed during the examination of receptor trees for the presence of dye; 2) dye did not move into all receptor trees directly grafted to the donor; and 3) dye did not move into any trees indirectly grafted to the donor. The latter two failures of the dye technique were illustrated on Stand 5 when plot 5-8, where dye had revealed two receptors, was partially excavated and the donor was found to be directly grafted to at least 4 trees and indirectly to a fifth. Also, on plot 5-12, dye failed to move from the donor, through an obvious graft, to a live stump which was in turn grafted to a vigorous living tree (Fig. 12). It is noteworthy that on this plot dye led to the detection of 2 stumps indirectly grafted to the donor. The behavior of isotopes under the above circumstances was not observed.

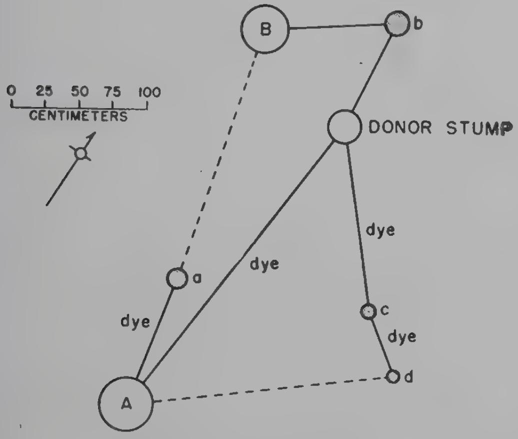


FIG. 12. Diagram of Plot 5-12 showing live trees as open circles, and those with dead tops and live roots as shaded circles. Solid lines mark grafts disclosed by dye transfer and/or excavation. Dotted lines indicate suspected grafts.

The failure of dye to move into all trees known to be connected to an injected tree raises questions regarding the forces governing movement between injected trees. Graham (1959) studied the rate of dye intake into collared stumps and correlated a sharp rise in intake with weather conditions favorable to increased transpiration. This suggests that stresses developed during transpiration are at least in part responsible for the movement of dye through grafts. The fact that dye will move to the tops of the standing boles of detopped elm trees, despite the absence of transpiring surfaces (Greenidge 1955b), indicates that other forces may also be involved in the transport of dye within single trees or between grafted trees. The failure of dye to move to all trees known to be grafted to donor stumps suggests that one or two trees, because of favorable stress gradients, or other factors, may dominate the root complex causing materials to be translocated to them at the expense of other members of the complex. Other possible explanations of this behavior are that not all grafts are functional, or that they function only under conditions not operative during the experimental period.

The common occurrence of more or less discrete groups of trees within various stands suggests that these represent clusters of trees bound together by a system of grafts. This point of view is supported by the excavations in Stand 5, and by the occurrence of clusters of intergrafted living stumps and trees (Fig. 12). The root complex found in Georges Pond Bog, where roots of 6 large trees are fused together in one anastomosing network (Fig. 7), may characterize many clusters found in upland situations, especially in older stands. In Scotch pine in Finland, Yli-Vakkuri (1953) has reported groups of 2 to 11 grafted trees to be common. Beskaravainyi (1956) reports that 50% of the trees in a 35- to 48-year-old pine plantation were grafted together in groups of 2 to 12 trees.

The naturally occurring white pine stand therefore may be visualized as being composed of clusters of grafted trees (unions) interspersed with individual trees without intraspecific grafts. The number of trees occurring in unions or as individuals in any stand is probably a function of spacing, with age and site being of some importance. In the extreme, it is conceivable that an entire stand may be united by a single anastomosing root network. In contrast, some open, widely spaced stands may be more or less free of intraspecific grafts.

A further manifestation of the prevalence of root grafts may be found in the common occurrence of live stumps whose roots are grafted to living trees. These clusters of living trees and stumps represent the mature phase of graft unions formed earlier in the life of the stand. Apparently, the trees that are the more aggressive members of a union survive, while weaker members die leaving only their roots to participate in the root complex. The fundamental question arises, after 2 trees become grafted together, can one utilize the root system of the other and perhaps contribute to the death of its top, or, conversely, can weaker trees and living stumps prolong their survival at the expense of their living companions?

Natural Root Grafting in other Forest Tree Species

A compilation of reports from the literature (Graham 1959) which lists 19 genera and 56 species of forest trees in which natural root grafting has been observed indicates that the findings or implications of the study may not be confined to white pine. The various genera and the number of species in each are as follows: Abies (5), Acer (3), Betula (6), Carya (1), Fagus (2), Fraxinus (1), Hevea (1), Larix (3), Liquidambar (1), Picea (2), Pinus (14), Populus (2), Pseudotsuga (1), Quercus (7), Sequoia (1), Thuja (2), Tilia (1), Tsuga (2), and Ulmus (1). In 40 of the 56 species listed, various workers estimated intraspecific root grafts and/or living stumps to be common. In addition, LaRue (1952) reported root grafts in 34 genera of trees growing in Puerto Rico.

Ecological Implications of Natural Root Grafting

The results of this study suggest that intraspecific competition may be overrated as a factor in determining which trees in a developing stand will survive. The relationship between members of a grafted union probably is not strictly one of intraspecific competition between plants occupying the same area and dependent upon the same physical factors. The nature of the union suggests that the participants have lost at least a part of their individuality, and may be subject to biochemical and biophysical influence by their grafted companions. A tree's ability to divert materials being translocated within the union may determine whether it will persist as a visible member of the stand or succumb to more vigorous companions, leaving only its roots to participate in the living union. A study of the comparative success of dominant and subdominant members of a union and non-grafted individuals is also needed.

Questions may also arise concerning the contribution of root grafting to the ability of a species to maintain its population status in a stand. Dominant trees, in some species, may assist their own seedlings or saplings through root grafts. This function is suggestion by the preliminary results of Kuntz and Riker (1956) who found that although radioisotopes moved in both directions between dominant and suppressed northern pin oaks, *Quercus ellipsoidalis* Hill, more often they moved from the dominant to the suppressed tree.

The development of self and/or intraspecific grafts may confer added resistance to windthrow as suggested by Pryor (1937) and Rigg and Harrar (1931). In bogs, swamps, thin soils, etc., where roots are restricted to the upper strata, the ability to develop a grafted root network might enable some species to persist where others fail.

Open spaces, left in the forest by the death of suppressed trees, are generally considered to be accessible for invasion. It seems, however, that such invasion may be retarded when the tops of some suppressed trees die and their much-grafted root systems continue to occupy the soil. It seems, also, that certain species may persist in areas where the normal supply of water and minerals is periodically limiting because, during that time, critical amounts are transported through root grafts from adjacent areas. For example, in riparian situations, trees some distance from the water may be maintained during periods of stress by water absorbed by streamside trees and transported through root grafts.

Practical Considerations

The widespread occurrence of root grafting among forest trees indicates the need for basic information by foresters. For example, the spurt of growth following thinning may be due to increased absorptive systems (Page 1927) and/or additional stored foods made available to the residual trees through grafts with the root systems of the thinned trees. Also, the increasing number of instances of "Backflash" (i.e., translocation of poison through root grafts to adjacent nonpoisoned trees, Cook and Welch 1957, Rushmore 1958, Wilcox, *et al.* 1956) indicates that a study of internal and external environmental conditions governing translocation through root grafts is prerequisite to sound forest management programs involving the selective use of silvicides. Finally, studies of the amount and rate of water movement through networks of grafted trees surrounding streams, lakes, and reservoirs should be of interest to hydrologists and watershed managers.

SUMMARY

1. A study of intraspecific root grafting in white pine was made.
2. A technique for detecting root grafts by a tracer method is described.
3. The major findings of the study were:

a. Root grafting occurs in white pine stands from 15 to 71 years of age, and probably in both younger and older stands.

b. Grafting occurs under a wide range of site conditions from bogs to dry sites.

c. Fusion may be limited to a single graft be-

tween trees, but often sizable clusters of trees are organically united by an extensive complex of self grafts and intraspecific grafts.

d. The degree of grafting in any stand is probably related to the age, density, and purity of the stand. Also, certain ecotypes may be more prone than others to the establishment of grafts.

e. Roots of seemingly dead trees often remain alive through grafts to living trees. This kind of multigenotypic entity is apparently common in many pine communities.

f. Many grafts are functional in the translocation of food, minerals, and water. Translocation of food was evidenced by the maintenance of growth in old living stumps. The translocation of water and minerals was demonstrated by the movement of dye and radioisotopes from tree to tree, from freshly cut stumps to trees, and from old living stumps to trees.

g. Some grafts may not function in translocation. This was shown by the failure of dye to move from cut stumps to adjacent trees known to be grafted to the stump.

It is suggested that in some instances grafted trees may behave as parts of an organic union rather than as individuals in competition with each other.

The number of reports of natural root grafting in many forest tree species suggests that the observations here reported and their ecological implications are not limited to white pine.

REFERENCES

Beskaravainyi, M. M. 1956. The formation of groups in pine plantings of the Kamyshinsk Forest Improvement Support Point (in Russian). Agrobiologiya **1956(1)**: 143-146. (Biol. Abstr. **32(11)**: 38517. 1958.)

Bormann, F. H. and B. F. Graham, Jr. 1957. Natural root grafting in woody plants. (Mimeo bibliography)

Cook, D. B. and D. S. Welch. 1957. Backflash damage to residual stands incident to chemi-peeling. J. For. **55**: 265-267.

Dickson, H. and V. H. Blackman. 1938. The absorption of gas bubbles present in xylem vessels. Ann. Bot. **2**: 293-299.

Franke, M. 1883. Beitrage zur Kenntniss der Wurzelverwachsungen. Beitr. Biol. Pflanz. **3**: 307-334.

Fraser, D. A. and C. A. Mawson. 1953. Movement of radioactive isotopes in yellow birch and white pine as detected with a portable scintillation counter. Canad. J. Bot. **31**: 324-333.

Graham, B. F., Jr. 1954. A technique for introducing radioactive isotopes into tree stems. Ecology **35**: 415.

———. 1959. Root-grafts in eastern white pine, *Pinus strobus* L.: Their occurrence and ecological implications. Ph.D. dissertation, Duke University.

Greenidge, K. N. H. 1955a. Observations on the movement of moisture in large woody stems. Canad. J. Bot. **33**: 202-221.

———. 1955b. Studies in the physiology of forest trees. III. The effect of drastic interruption of conducting tissues on moisture movement. Amer. J. Bot. **42**: 582-587.

Kuntz, J. E. and A. J. Riker. 1956. The use of radioactive isotopes to ascertain the role of root grafting in the translocation of water, nutrients, and disease inducing organisms among forest trees. Proc. Int. Conf. Peaceful Uses of Atomic Energy (Geneva, Switzerland). **12**: 144-148.

LaRue, C. D. 1934. Root grafting in trees. Amer. J. Bot. **21**: 121-126.

———. 1952. Root grafting in tropical trees. Sci. **115**: 296.

Morris, R. F. 1951. Tree injection experiments in the study of birch dieback. For. Chron. **27**: 313-329.

Neeff, F. 1922. Über polares Wachstum von Pflanzenzellen. Jb. Wissensch. Bot. **61**: 205-283.

Newins, H. S. 1916. The natural root grafting of conifers. Proc. Soc. Amer. For. **11**: 394-404.

Page, F. S. 1927. Living stumps. J. For. **25**: 687-690.

Pryor, L. D. 1937. Some observations on the roots of *Pinus radiata* in relation to wind resistance. Aust. For. **2**: 37-40.

Rigg, G. B. and E. S. Harrar. 1931. The root systems of trees growing in sphagnum. Amer. J. Bot. **18**: 391-397.

Roth, C. 1896. Eine Methode der kunstlichen Baumernahrung. Chem. Zeitschr. **20**: 344-345.

Rubtsov, N. I. 1950. New data on the grafting of root systems of certain forest species (transl. title). Agroibologiya **6**: 57-65.

Rushmore, F. M. 1958. Sodium arsenite in spaced ax cuts: an effective stand-improvement technique. J. For. **56**: 195-200.

Shevyrev, I. 1894. Extraradicate nutrition of diseased trees. Bot. Div., St. Petersburg Imp. Soc. Nat. Conf.

Sinnott, E. W. 1952. Reaction wood and the regulation of tree form. Amer. J. Bot. **39**: 69-78.

Stoddard, E. M. and A. E. Dimond. 1949. The chemotherapy of plant diseases. Bot. Rev. **15**: 345-376.

Thimann, K. V. 1958. The physiology of forest trees. Ed. by K. V. Thimann. Ronald Press. N.Y.

True, R. P., T. M. Judy and E. Ross. 1955. The absorption of solutions through the tops of freshly cut oak stumps. W. Va. Agric. Exp. Sta., Current Rep. **11**.

Wilcox, H., F. J. Czabator, G. Girolami, D. E. Moreland and R. F. Smith. 1956. Cemical debarking of some pulpwood species. N.Y. St. Coll. For. Techn. Publ. **77**.

Yli-Vakkuri, P. 1953. Tutkimuksia puiden välisistä elimellisistä juuriyhteyksistä männiköissä. (With German summary: Untersuchungen über organische Wurzelverbindungen zwischen Bäumen in Kiefernbeständen). Act for. fenn. **60**: 1-117.

REVEGETATION OF LANDSLIDES IN THE WHITE MOUNTAINS OF NEW HAMPSHIRE[1]

Edward Flaccus[2]
Department of Botany, Duke University, Durham, N. C.

Introduction

Landslides, although of particular concern to geologists, geomorphologists and hydrologists, have also interested students of vegetation; such mass-movements provide opportunity for study of succession (Langenheim 1956) and possible effects of vegetation on their occurrence (Ellison and Coaldrake 1954; Japanese Government Forest Experiment Station 1956).

This paper reports part of a comprehensive study of landslides and their revegetation in the White Mountains of New Hampshire during 1956 and 1957. The history, characteristics, and causative factors of the slides are considered elsewhere (Flaccus 1958, a & b). Landslides in the White Mountains are of the debris-avalanche type and their scars are conspicuous features of the mountain scenery (Figs. 1 & 2). Occurring during intense summer rains, these slides are sudden mass-movements initiated by sliding on the steep upper slopes and continuing downward as flow movement of earth, rocks, and vegetation, mixed with large amounts of water. There are records of slides since the area was first settled; sometimes destructive, two of them have caused loss of life. Aerial photographs of the region show the scars, in varying stages of healing, of more than 500 slides. Slides of the debris-avalanche type have also occurred in the Katahdin Range of Maine, the Adirondacks of New York, the Green Mountains of Vermont, the Berkshires of Massachusetts, and the southern Appalachians in Virginia and North Carolina.

Succession can be studied on a single area (Lakela 1939; Langenheim, 1956), but generalizations must be made with care, and such studies are most valuable when extended over a period of years. Another approach is to study a number of areas of various ages and reconstruct the succession, as done by Keever (1950) on old fields, Leisman (1957) on spoil banks, and Olson (1958) on Lake Michigan dune areas. This approach requires care because of variation in factors other than time; in the present study, it is supplemented by detailed analyses of single areas.

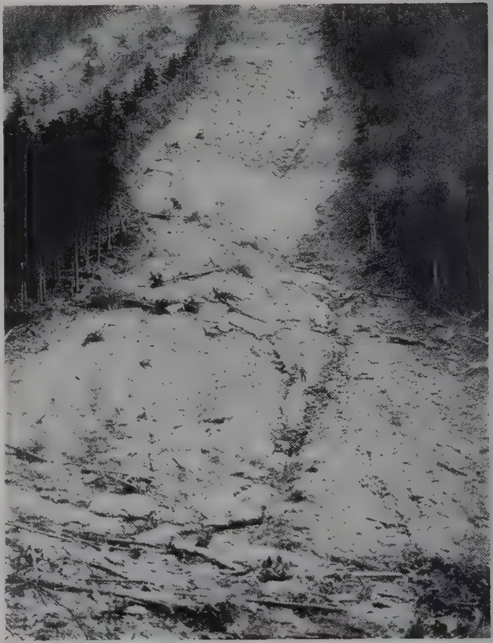


Fig. 1. North Tripyramid slide of August, 1885. This picture was probably taken within a few weeks after occurrence. The large slide turned in the area of the photo foreground and carried its destructive load for 2 miles down a brook. Note man standing, a little below and to the right of the center of the picture (photo courtesy Appalachian Mountain Club).

Tree species are referred to in the text by common name for convenience (they are paired with scientific names in Table II), while scientific names are used for all shrubs and herbs. All nomenclature is that of Gray's Manual (Fernald 1950). Voucher specimens have been deposited in the herbarium of Duke University.

The writer wishes to acknowledge the financial assistance of the National Science Foundation and the Northeastern Forest Experiment Station. Thanks are due to District Rangers of the White Mountain National Forest and the staffs of the Franconia Notch State Reservation, the Soil Conservation Service county offices, and of the Northeastern Forest Experiment Station for facilitating

---

[1] Part of a thesis submitted to the graduate faculty of Duke University in partial fulfillment of requirements for the degree of Doctor of Philosophy.

[2] Present address: Department of Biology, University of Minnesota, Duluth Branch, Duluth, Minnesota.

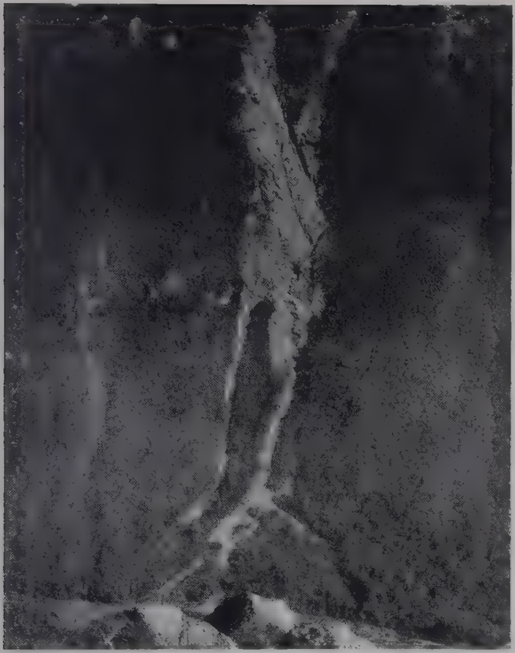


Fig. 2. Franconia Notch slide of June, 1948, as it looks 9 years after occurrence. This slide is about 0.8 mi. long. Note 2 old scars to right, mostly healed with hardwood growth (esp. white and yellow birch), of slides believed to be about 50 years old (photo by author).

field work; to the Appalachian Mountain Club for use of their historical material and photos; to the Soil Testing Division of the North Carolina State Department of Agriculture for performing soil analyses; to Dr. Albion Hodgdon of the Botany Department of the University of New Hampshire for checking plant identifications; and finally to Dr. H. J. Oosting of the Department of Botany, Duke University, for support and guidance in all phases of the work.

The Study Area

The study area was limited to include the "White Mountains," but excluding the Moosilauke-Kinsman Ranges. Roughly, then, this study covers the mountainous region east of the Pemigewasset River, south of the Israel and Androscoggin Rivers, west of the Maine border, and north of the Bearcamp River (Fig. 3).

The White Mountains are the eroded remains of several series of plutonic, granitic intrusions and the older sediments that were metamorphosed into schists and gneisses before or at the time of these intrusions. Bedrock is therefore of two general types: (1) plutonic, including especially granites, syenites, and monzonites, and (2) metasedimentaries, including mica schists and gneisses.

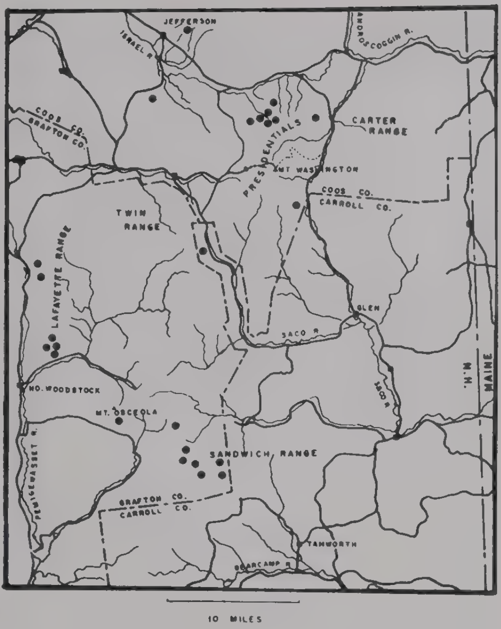


Fig. 3. Map of study area. Dots represent approximate locations of slides visited.

The mountains, though for convenience often grouped into the Carter-Moriah, Presidential, Twin Mt., Franconia, and Sandwich Ranges, occur in an irregular mass dissected in almost all directions by streams of the Connecticut, Androscoggin, Saco, and Merrimack drainages. Altitudes of the major peaks range mostly from 3000 to 5000 ft., but Mt. Washington, highest in the Northeast, reaches 6288 ft. above sea level.

Lower slopes and valleys are covered with glacial till or stratified drift of varying thickness, attributed to the Wisconsin Stage, and there are local areas of till at higher altitudes (even on the summit of Mt. Washington). But for the most part the higher altitudes expose bedrock, either bare or covered with joint-blocks, and the high altitude coniferous forests grow directly on this rock, with little or no soil development. Wherever soils do develop, they become strongly podsolized, especially under coniferous growth.

The climate is cool in summer, cold in winter, and precipitation is fairly evenly distributed throughout the year, though slightly higher during the summer months. Annual preciptation averages mostly between 40 and 60 in., but these values may be exceeded at the higher elevations. Snow cover lasts from November-December to April-May, depending on altitude; in some spots on Mt. Washington it may persist into July.

Westveld's (1956) classification of forest vegetation zones in New England provides a useful framework for characterizing the forests of the White Mountains. Most of the region lies in his Zone I: Spruce-Fir-Northern Hardwoods. Hardwoods, especially beech, sugar maple, and yellow birch, grow on the lower slopes, with varying and minor admixtures of red spruce, fir, hemlock, red maple, ash, paper birch, and scattered white pine. All of these are referrable to Westveld's Tolerant Hardwoods-Spruce-Fir Subdivision. As a result of lumbering, the proportion of spruce on these lower slopes has been severely reduced. The upper slopes are referrable to the Spruce-Fir-Intolerant Hardwoods Subdivision; they are covered with stands of red spruce, fir, and combinations of the two, with varying admixture of paper birch (variety *cordifolia*). Upwards to the highest altitudes, red spruce drops out, leaving pure fir or fir-paper birch, becoming increasingly stunted to timberline. Timberline is usually a gradual merging of the krummholz with the alpine tundra which occurs above about 5000 ft. Black spruce is associated with the fir at timberline.

The transition from the lower to the upper subdivision of the Spruce-Fir-Northern Hardwoods Zone is gradual. Though somewhat arbitrary, the altitudinal limits within which this transition takes place may be set at 2000-2500 ft. Observations indicate that beech and sugar maple, which gradually decrease in numbers and size upwards, tend to disappear within this altitudinal range. Such altitudinal limits agree with those of Hodgdon and Steele (1958). The typical low-altitude variety of paper birch does not usually occur much above 2000 ft., and is replaced upward by the *cordifolia* variety.

Within both subdivisions of Zone I, the pioneer tree species listed by Westveld are pin cherry, trembling aspen, and paper birch. In the lower subdivision, yellow birch and red maple should probably be added as pioneer species, because of their role in slide revegetation.

Considerable white pine grows on the larger intervales, either mixed with hardwoods or in pure second-growth stands. Such areas are referrable to Westveld's Zone II: Northern Hardwoods-Hemlock-White pine. Here gray birch joins the other pioneer species.

METHODS

In the course of the study, 29 slides were visited; general observations of revegetation and surrounding vegetation were made, and presence lists were accumulated. To get a more precise idea of the progress of revegetation, sampling was done on 7 slides representing a chronoseries of the following dates of occurrence: 1885, 1897, 1927, 1938, and 1948 (72, 60, 30, 19, and 9 years old respectively). Sampling was confined to areas of deposit, and the detailed results are hence applicable only to those areas of the slides capable of rapid and complete revegetation. The chronoseries slides were among 135 that were dated to the year by historical research, confirmed in some cases by tree-ring analysis (Flaccus 1958a).

It was necessary to select a sampling method for the trees that would produce information, usable in comparisons, on a series of stands of great age difference, ranging from sapling thickets to mature forests. Limited time made one of the distance systems seem desirable, though they are not suitable for very young stands. A compromise solution was chosen using a combination of a distance method and quadrats.

The point-centered quarter method (Cottam, Curtis and Hale 1953; Cottam and Curtis, 1956) was used for all trees one in. DBH and over, on all areas except those of the 1948 (9-year-old) slide, where trees were too small. Points were located at 5-pace intervals (in the oldest stands at 10-pace intervals) along lines which followed selected compass directions, and were placed at varying distances from each other by use of random numbers. At each point a m^2 quadrat was also laid out for all trees less than one in. DBH, and for all shrubs and herbs. Trees $<$ one in. DBH on these quadrats were recorded as to number of stems of each species, and the height of each stem was estimated to the nearest half foot. Shrubs were recorded as to number of stems, and herb presence only was recorded. There are, then, two bodies of data for each sampled area (except for those of 1948, for which quadrat data only were obtained): (1) quarter data, consisting of recorded species, DBH, and distance from the point of four trees one in. DBH or larger for each point, characterizing the dominant layers; and (2) quadrat data, consisting of species and number of stems of shrubs and of trees $<$ one in. DBH, and presence of herb species. The quadrat data therefore apply to tree reproduction, shrub, and herb layers.

Since sampling was done late in the season, delicate vernal herb species may be slightly underrepresented. Vascular cryptogams (ferns, club mosses) were recorded to species. No attempt was made to distinguish species or genera of mosses, except that two genera, Sphagnum and Polytrichum, were recorded separately.

Soil development on the chronoseries was also studied. To get an idea of changes with time in pH, organic matter, and availability of certain mineral nutrients, samples of soil were collected from deposit areas of the Franconia Notch So., Pinkham, and Tripyramid No. slides, and from some of the barrens areas. Samples were also taken from the mature forests surrounding each of the slide areas. From each of three to five separate pits on each area, two samples were taken, one from the top 2 in. layer, the other from the 2-4 in. layer (depth being reckoned from the top of the F layer). The dried samples were passed through a 2 mm. sieve, and the portions < 2 mm. were tested for pH, organic matter, exchangeable calcium, magnesium, potassium, and for available phosphorus. These tests were performed by the Soil Testing Division of the North Carolina Department of Agriculture.

Because of the great variability of size of mineral particles in the deposit areas, mechanical analysis of the soil samples was not considered worthwhile.

General Revegetation

Slide habitats may be classified into the following types: (1) bare cliffs and ledges, (2) rock debris and talus deposits at the foot of the ledges and steep places, (3) areas of erosion in glacial till, (4) residual areas, (5) areas of alluvial deposit. The expected location of these habitats on a generalized slide is diagrammed in Fig. 4. There is variation among such primary slide characteristics as slope, compass exposure, parent rock or till, geographical location, previous history of surrounding vegetation, time of occurrence, and resulting drainage pattern. Surprisingly, the process of slide revegetation is not as complicated as this web of factors suggests. On many habitats the successions are rather uniform, and are at least amenable to broad characterization. The reason for this is that all slide sites at first are exposed to high light, high transpiration stress, extremes in temperature, and many are affected by instability of root medium and susceptibility to subsequent water erosion. Pioneer species appear to have broader ecological amplitude than terminal species; the relatively few pioneers involved in slides can colonize a variety of habitats, making for similarity of successions in spite of variation in ecological factors. On the five habitats listed above, revegetation is very slow on the bare ledges and the rock debris deposits below them, may be slow or rapid on areas of erosion in glacial till, and is comparatively rapid on the residual and deposit areas. Discussion of revegetation of the first four types is based on general observations made on all slides visited. The last type, areas of deposit, was studied by sampling techniques, and will be considered in detail in a subsequent section.

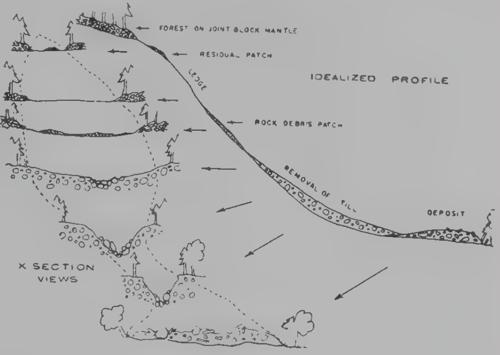


Fig. 4. Diagrammatic profile and face view of generalized slide, showing slide habitats.

Bare cliffs and ledges

No attempt was made to study moss and lichen stages on bare rock. Mosses and lichens were slow in appearing on the rock surfaces, none being in evidence on the ledges of the 3-year-old slides (Osceola; King Ravine), nor of the 9-year-old slides (Franconia Notch). Some mosses and lichens were noted on the ledges of Passaconaway SE slide (19 years old) and those of Whiteface North slide (about 35 years old).

In cracks, crevices, or small sediment-collecting pockets, invasion is much quicker, by any of a number of possible pioneer species ranging from certain mosses to species of grass (e.g. *Agrostis scabra*), sedge (e.g. *Carex brunnescens, C. debilis* var. *rudgei*), rush (*Luzula parviflora, Juncus trifidus, J. effusus*), herbs (*Drosera rotundifolia, Hieracium* sp., *Viola* sp., *Aster acuminatus,* and *Anaphalis margaritacea*), shrubs (*Diervilla lonicera, Rubus idaeus*), and tree seedlings (esp. *Betula papyrifera* var. *cordifolia,* red spruce, balsam fir). Given a crevice with a small amount of soil any of these species is capable of coming in immediately following slide occurrence. Even so, development is apt to be extremely slow on such areas, since they are usually on upper, steeper parts of the slides, where exposure to wind appears to limit growth.

Talus deposits at the foot of ledge sections

Reference is made here only to those talus deposits associated with slides. These deposits lie at the foot of the steep ledges and cliffs of the slides, and consist of patches of rock rubble. The rubble is continually added to by disintegration processes which occur on the ledges above. The fragments may be large or small, are more or less sorted by colluvial action, and are subject to some bombardment from above. The substrate is therefore unstable and revegetation is sparse. The root systems of herb species available are apparently unable to cope with such instability. Scattered plants of paper birch (var. *cordifolia*), pin cherry, yellow birch and raspberry become established, but are frequently chlorotic.

Areas of erosion in glacial till

In the upper and middle slide-sections broad areas of till may be exposed by the sliding action. The slope is steep, resulting in instability. Exposure to wind and temperature extremes is usually severe. Revegetation, mainly by paper birch (var. *cordifolia*), red spruce, and fir is so poor that many of these areas can appropriately be termed "barrens." On the barrens, growth is extraordinarily stunted and often chlorotic. The birches periodically die back to the base. The spruces and firs may be quite thickly stocked, but show severe stunting, chlorosis, downslope flagform of foliage, creep-curve in the root-stem transition zone, and contorted, blackish stems with increased size and frequency of resin blisters. Although growing in the open, 20-year-old stands were often about one foot high.

Farther down, where the erosion in till is deeper, gullies are produced which have U to V cross-sections. If the sides are not too steep, revegetation can be quite satisfactory, involving all the common tree pioneer species: paper and yellow birch, trembling aspen, and pin cherry. Mountain alder (*Alnus crispa*), bigtooth aspen (*Populus grandidentata*), and the various species of willow are often present in lesser numbers in the early stages. Spruce and fir may develop under the pioneers. Success of species on these sites is probably a function of stability, available moisture, accumulation of organic debris, and protection from extreme exposure.

On the steep sides of the V gullies, instability of substrate may interfere seriously with revegetation. Bare areas comparable to the faces of gravel or sand pits (or ungraded road-cuts) result, and may persist for long periods. Patches of humus complete with growing plants are frequently undermined at the top of the banks and "migrate" slowly downslope. This is part of the process of slope reduction, and the patches help in eventual revegetation.

Running through the upper eroded areas, gullies of boulders develop as the finer till components are washed away. Nothing grows here, but downward the gullies usually become intermittent to permanent brooks, along which grow various grasses, sedges, rushes, forbs, and trees (esp. various species of willows: *Salix bebbiana, S. discolor, S. nigra, S. rigida,* etc.).

Residual areas

The slide process may leave islands of vegetation on which the forest growth remains undisturbed, or from which which the vegetation has been more or less "shaved." The trees along the edges of such islands or of the slide itself may be injured by being barked, by having parts of the root systems torn away, or by having the roots exposed to subsequent drying due to exposure of the soil. The subsequent growth on such sites may be slowed by increased drainage and exposure.

There are many smaller patches from which the vegetation has been torn, leaving duff and soil held in position by tree roots that are well anchored in the underlying ledge crevices. These patches tend to occur toward the slide edges, on relatively high ground, or in the lee of large ledge promontories or boulders that have held against the sliding debris. They are easily recognized on the more recent slides. Various terminal herb species (e.g. *Cornus canadensis, Clintonia borealis, Aralia nudicaulis, Dryopteris spinulosa*) may be left growing, but these usually show chlorosis and decline in vigor within a year or two, presumably because of the sharp change to a drier and more exposed habitat. Persisting shrubs of broader ecological tolerance (*Rubus idaeus, Vaccinium* spp. blueberry, and *Sambucus pubens*) may enjoy a flush of growth, accompanied by the appearance of some pioneer sedges, grasses, and forbs. Mountain maple and mountain ash (Pyrus spp.) frequently sprout from persisting bases. Pin cherry is the most common tree species, growing from seed that was "banked" in the duff. A high proportion of the pin cherry reproduction on slides grows on residual areas.

Deposit areas

These sites are heterogeneous mixtures of boulders, gravel, sand, and organic matter (mostly macerated trees), and may be laid down as "moraines," ridges, or beds in various parts of the slide. Most often, they occur toward the bottoms of the slides, where reduced slope angle slowed velocity and resulted in deposition. They occur intermittently along the lower reaches of the stream scours. They are often largest at the bottoms of those slides which do not empty into permanent streams. These deposit areas are easy to recognize on the more recent slides (30 years old or less), since they invariably have chewed-up tree fragments mixed in with the mineral debris. On older slides this distinguishing feature disappears, but the deposits can often be recognized by position and shape.

As a result of position, mild slope, and the incorporation of organic matter, these deposits are capable of more rapid and thorough revegetation than any other type except residual areas.

Presence

Presence lists were compiled on 22 of the 29 slides visited. Full lists, giving % presence of all species, are presented elsewhere (Flaccus 1958a). No meaningful use can be made of the number of species occurring on a slide as related to age, since number of species is directly affected by size of slide and nature of habitats, both of which vary a great deal. Even though the basis varies with size, age, diversity of habitat, and number of visits, % presence is still a general measure of the commonness of species. A total of 31 tree species, 16 shrub species, and 105 herb species were recorded from the 22 slides (these figures are minimal and approximate because some plants were not determined below the genus level and were counted as single species). Tree species with highest presence were paper birch (100%), pin cherry (100%), yellow birch (95%), red spruce (91%), balsam fir (86%), trembling aspen (86%), and mountain maple (82%). Only 3 shrub species exceeded 50% presence: *Rubus idaeus* (91%), *Spiraea latifolia* (55%), and *Spiraea tomentosa* (50%). Among the herbs with highest presence were *Aster acuminatus* (86%), *Anaphalis margaritacea* (77%), *Dennstaedtia punctilobula* (68%), *Solidago graminifolia* (59%), *Carex debilis*, var. *rudgei* (55%), and *Agrostis scabra* (50%).

The species with high presence values include a high proportion of pioneer, light-demanding shrubs and herbs relative to terminal, shade-tolerant types. The reason is that most slides of the age-range studied possessed at least some open, exposed habitats suitable for pioneers.

High presence values do not necessarily mean that a species is ubiquitous in the sense of being able to grow on a variety of habitats. *Anaphalis margaritacea*, for example, although it has a high presence percentage, is actually a light-demanding pioneer that disappears quickly with the development of a tree canopy. *Aster acuminatus*, on the other hand, maintains substantial frequency in both early and late stages of deposit area succession, and hence is classified as a true ubiquist (*sensu* Rowe 1956). The difference between these two species is reflected in the chronoseries data presented later (Table V).

SUCCESSION ON DEPOSIT AREAS

Evidence from the chronoseries

Vegetation was sampled intensively on a chronoseries of deposit areas (Table I). Data for tree species on the 1938 (19-year-old) sites were recognized as unreliable for comparison: since most trees on such sites were about one in. DBH, m² quadrats do not represent the canopy adequately and the quarter data give undue weight to species which first exceed one in. DBH (trembling aspen, pin cherry, and white birch) and not enough weight to the slower growing yellow birch.

TABLE I. Chronoseries deposit areas sampled

Area	Age, yrs.	Altitude, ft.	No. of points
Tripyramid	72	2730	11
	72	2660	39
	72	2550	11
Cherry Mt.	72	1890	20
Osceola	60	2220	12
	60	2270	9
Pinkham Notch	30	2300	18
	30	1660	20
Madison Scout	19	2955	9
	19	2925	8
	19	2800	10
Big Coolidge	19	1500	16
	19	1500	15
	19	1400	12
Franconia Notch	9	3275	11*
	9	2800	8*
	9	2300	14*
	9	2240	13*
	9	2175	10*
	9	2075	10*

* Quadrat data only.

Relative density, relative frequency, relative dominance (of basal area), and their summation, the importance value, were calculated by the usual methods (Curtis and McIntosh 1951; Cottam and Curtis 1956) for each tree species of the 30-, 60-, and 72-year-old areas. Importance values are listed in Table II, with species arranged from most pioneer to most terminal (the two subordinate layer maples are separated from this ranking).

Since quadrat data only are available from the youngest (9-year-old) area, there are no basal

TABLE II. Importance values of tree species over latter part of chronoseries (based on point-quarter data)

		Age of Area in Years		
		30	60	72
no. of areas averaged...		2	2	4
Prunus pensylvanica...	pin cherry	11	—	—
Salix bebbiana.........	bebb's willow	12	—	—
Populus tremuloides....	trembling aspen	7	10	6
Betula papyrifera......	paper birch	140	45	58
Betula lutea...........	yellow birch	103	103	75
Picea rubens..........	red spruce	12	77	55
Abies balsamea........	balsam fir	14	44	72
Acer saccharum........	sugar maple	—	—	9
Fagus grandifolia......	beech	—	—	2
Acer pensylvanicum....	moose maple	—	6	12
Acer spicatum.........	mountain maple	3	—	13

area values for this age group. Relative frequencies are not comparable to those of older groups since percentage frequency of the quadrat method is not the same as percentage frequency of the quarter method (Curtis and McIntosh, 1951). Relative density values from quadrats were assumed to be at least roughly comparable to those from point-quarters, and a comparison of these values over the whole chronoseries is made in Table III.

TABLE III. Relative densities of tree species over the chronoseries. All values are based on point-quarter data except those of 9-yr.-old group, which are based on m² quadrat data

	Age of Area in Years			
	9	30	60	72
no. of areas averaged.........	6	2	2	4
Prunus pensylvanica...........	2	4	—	—
Salix bebbiana.................	—	1	—	—
Populus tremuloides...........	1	1	1	1
Betula papyrifera.............	49	44	11	13
Betula lutea..................	45	42	32	22
Acer rubrum..................	—	—	4	—
Picea rubens.................	2	4	37	24
Abies balsamea...............	1	4	15	27
Acer saccharum...............	—	—	—	3
Fagus grandifolia............	—	—	—	1
Acer pensylvanicum...........	—	—	1	4
Acer spicatum................	—	1	—	6

Evidence from stand structure

Additional information concerning the progress of revegetation can be gained from the structure of the 72-year-old stands. The data of the four 72-year-old areas were pooled to make one "composite stand," and the relative density, relative frequency, relative dominance, and importance value calculations made using the combined data. By doing this it was possible to break the trees > 1″ DBH down into two size classes: the 1-3.9″ DBH class and the > 3.9″ DBH class, and still have a large enough sample in each for valid results. The relative values and their summations are given in Table IV, along with relative density values for the < 1″ DBH class. An increase in canopy importance of yellow birch, red spruce and balsam fir is a reasonable prediction of potential succession beyond 72 years. Use of the < 1″ DBH values for longer term prediction is not justified; about all one can say is that aspen and white birch will drop out completely until the canopy is again opened by windthrow, fire, lumbering, or new slides.

TABLE IV. Structure of composite 72-yr.-old stand (combination of 3 areas on Tripyramid North Slide and one area on Cherry Mt. Slide)

	>3.9″ d.b.h. (81 points)				1-3.9″ d.b.h. (81 points)				<1″ d.b.h. (70 quadrats)	
	Relative density	Relative frequency	Relative dominance	Importance value	Relative density	Relative frequency	Relative dominance	Importance value	Relative density	Relative frequency
Populus tremuloides........	4	4	7	15	—	—	—	—	—	—
Betula papyrifera..........	35	35	38	108	3	4	5	12	—	—
Betula lutea...............	25	23	25	73	11	12	14	37	3	3
Picea rubens..............	6	6	3	15	42	37	35	114	4	9
Abies balsamea............	26	26	24	76	32	33	36	101	44	27
Acer saccharum...........	1	1	—	2	3	4	3	10	9	17
Fagus grandifolia..........	1	1	—	2	—	—	—	—	—	1
Acer pensylvanicum........	4	5	2	11	3	4	2	9	13	17
Acer spicatum.............	—	—	—	—	7	6	6	19	27	23

Effect of altitude

Some idea of differences in revegetation with altitude on a single slide can be gained from the Franconia Notch data. The altitudes of the six areas sampled on this slide are given in Table I. For all these areas the surrounding vegetation falls into the general category of spruce-fir-birch (both white and yellow birch), but proportions of these species change with altitude: white birch, spruce, and fir are more numerous at higher altitudes, while yellow birch is more numerous at lower.

The change with altitude of the relative densities for the most important tree species on the sampled deposit areas of this slide are given in Fig. 5. The two birches are very abundant compared to all other species; the proportion of yellow birch to white birch increases downward as expected. In addition to density and frequency data, the maximum height of each species in each quadrat was recorded. These values, averaged for the respective altitudes to give average maximum heights, are diagrammed in Fig. 6. Pin cherry and aspen far outrank the birches in speed of growth, but all species show reduced height growth rate at higher altitudes.

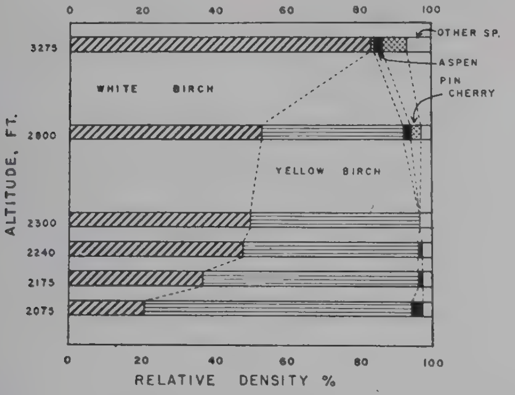


FIG. 5. Relative density of tree species on 9-year-old slide, in relation to altitude.

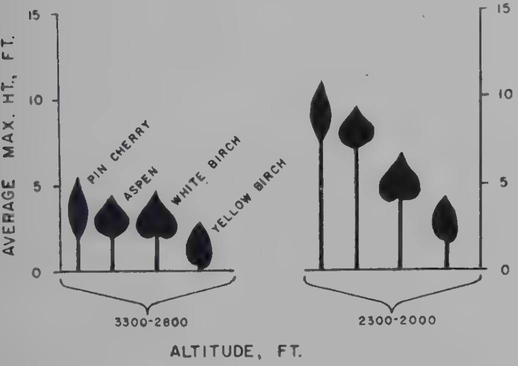


FIG. 6. Height growth of 4 pioneer tree species on 9-year-old slide in relation to altitude.

Herb succession

In the earliest stages of revegetation, the existence of a grass-sedge-forb stage of any extent is problematical. Slides of each age group up to about 6 or 7 years would be necessary to characterize these early stages accurately. Since such were not available, only tentative judgments can be made. There appears to be no herb dominance stage covering an appreciable area. The pioneer species of this life form are present on the 3-year-old slides, but their distribution is sporadic and their cover usually negligible. Fairly extensive cover of this type did appear on parts of a slide believed to be about 5 years old (Starr King E.), but even here it was not thick enough to appreciably delay the tree seedling growth. Because of instability and stoniness, most slide areas are not suitable for extensive development of the species of herbs available. Dense, small "stands" may exist in well-watered patches, but beyond about 5 years they can exist only locally, as, for example, mats of perennials along brook edges.

Table V gives the percentage frequency of herbs in the deposit area quadrats. Values given are averages for each age group. Because many of the herb specimens were in vegetative condition, it was necessary to record certain of them as genera only (some specimens of light-demanding species were so suppressed as to present even poorly developed vegetative parts). No species are given for *Viola, Goodyera, Juncus, Luzula, Epilobium, Hieracium,* and *Fragaria.* Grasses and sedges are indicated to family only, and mosses are simply noted as such, except for the genus *Polytrichum.*

Because there are not enough samples in some

TABLE V. Percent frequency of herbs of the chronoseries (averaged for each age group)

	AGE OF AREA IN YEARS				old
	9	19	30	72	(>200)
Juncus spp.	8	—	—	—	—
Luzula spp.	3	—	—	—	—
Epilobium spp.	8	—	—	—	—
Hieracium spp.	8	—	—	—	—
Rumex acetosella	5	—	—	—	—
Achillea millefolium	3	—	—	—	—
Fragaria spp.	3	—	—	—	—
Solidago graminifolia	6	—	—	—	—
Anaphalis margaritacea	8	—	—	—	—
Polytrichum spp.	61	21	14	1	3
Dennstaedtia punctilobula	27	4	—	3	—
Dryopteris phegopteris	16	4	—	2	5
Aster acuminatus	29	21	—	30	30
Viola spp.	6	21	—	32	30
Tiarella cordifolia	—	—	—	8	—
Solidago macrophylla	(5)*	—	—	15	—
Solidago flexicaulis	—	—	—	9	—
Dryopteris noveboracensis	—	—	—	2	—
Dryopteris disjuncta	—	—	—	2	—
Prenanthes spp.	(2)	—	—	17	8
Galium spp.	—	—	—	9	3
Maianthemum canadense	—	—	—	12	6
Dryopteris spinulosa	—	(18)	—	33	28
Goodyera spp.	—	—	—	4	3
Aralia nudicaulis	—	—	—	5	6
Rubus pubescens	—	—	—	9	17
Clintonia borealis	—	—	—	13	25
Trientalis borealis	—	—	—	3	15
Oxalis montana	(4)	—	—	4	27
Eupatorium rugosum	—	—	—	—	14
Trillium spp.	—	—	—	—	18
Medeola virginiana	—	—	—	—	12
Uvularia sessilifolia	—	—	—	—	23
Athyrium Filix-femina	—	—	—	—	9
Lycopodium lucidulum	—	—	—	—	21
Lycopodium obscurum	—	—	—	—	3
Cyperaceae	66	29	—	5	14
Gramineae	45	—	—	2	25
mosses other than *Polytrichum*	11	—	19	12	5

* Values in parenthesis represent clearly persisting specimens that were growing on patches of residual duff.

of the age groups, and because frequency measures dispersion but not necessarily abundance, this table is suggestive only of general floristic trends. Species have been arranged in order suggested by their frequency values, the most pioneer at the top, the most terminal at the bottom. Sedges, grasses and mosses, being composites of many species, are segregated at the bottom. The low values registered by the pioneer herb species in this table reflect the fact that already at 9 years a thicket of pioneer trees is crowding out the herbs.

The data show an extreme paucity of herb species on 19- and 30-year-old areas—far fewer than in either earlier or later stages. The general situation is probably as follows: a variety of pioneer, light-demanding species persists into the early stage of dominance by sapling tree growth but are gradually choked out. There seems to be an intermediate condition of too much shade for pioneer herbs but not sufficient soil development, or concomitant increase in soil water and available nutrients, to support most shade-tolerant, mesophytic species. In the later stages there is again a wide variety of species, but it is a spectrum of shade-tolerant types that may have higher requirements for organic matter, moisture, and nutrients in the soil. At 72 years the herb spectrum is already similar to that of the surrounding forests ("old" column, Table V). As mentioned earlier, *Aster acuminatus* is a ubiquitous species; it is almost the only one indicated by these data, except for *Dryopteris phegopteris* and possibly *Viola* (if a single species). The other species show marked association with either pioneer or terminal habitats.

Shrubs

By the time a densely stocked pioneer tree thicket is established, as in the 9-year-old Franconia Notch stands, shrubs are inconspicuous. Raspberry (*Rubus idaeus*) still shows a reasonably high frequency, but the plants are suppressed. A few other species may be present, such as *Diervilla lonicera, Spiraea latifolia,* and *Spiraea tomentosa,* but are scarce in numbers and suppressed; the latter two especially are light-demanding, and therefore transitory. Raspberry persists in the older areas of the chronoseries, but its frequency is much reduced in the later stages. Other than raspberry, no shrubs at all were present in the intermediate (19-year-old, 30-year-old) aged sampled areas. On 72-year-old sites, *Rubus idaeus, Diervilla lonicera,* and *Sambucus pubens* were present, but all with very low frequency.

Observation on mature stands in the region indicates that shrubs are generally unimportant to non-existent in heavily stocked, even-aged stands, somewhat more important but still limited in all-aged forests such as old-growth and virgin stands, and locally important in areas disturbed by windthrow, lumbering, and fire. The species involved are *Nemopanthes mucronata, Rubus idaeus, Ribes* sp., *Vaccinium* (blueberry) spp. in the spruce-fir and spruce-fir-paper birch forest types of higher altitudes, and *Rubus idaeus, Viburnum alnifolium, Sambucus pubens* and others in the various softwood-hardwood mixtures at lower altitudes. In disturbed areas particularly, the subordinate tree species (moose maple, mountain maple, and mountain ash) may behave as shrubs for long periods.

In areas subjected to windthrow and lumbering, the shrub layer that exists is largely undisturbed and at the same time is released from suppression; hence it becomes important locally for at least a time. On slide deposits, however, everything must start at once from seed. The pioneer tree species, with greater seed sources and generally greater seed mobility, come in much more thickly. The shrub species are sporadic in the first few years, and are progressively reduced as the pioneer tree thicket develops.

Soil development on the chronoseries

Results of the soil analyses are given in Table VI. Unfortunately, the parent materials of the soils are different, introducing an important variable other than time. Neverthless, the analyses supply quantitative values for the tested character-

TABLE VI. Soil analyses. Each value is that of a composite sample from 3 to 5 pits on the particular area. Those designated as old are from forests surrounding the slides (on basis of vegetation, at least older than 200 years). Methods: exchangeable Ca, Mg, K by photometer, 1.0 N. $NH_4C_2H_2O_3$; organic matter by $Na_2Cr_2O_7-H_2SO_4$ wet digestion; pH by glass electrode

		EXCHANGEABLE IN ME/100 G.			ORGANIC MATTER	
	Age of area	Ca	Mg	K	%	pH
0-2″ LAYER						
Franconia Notch....	9	0.400	0.060	0.130	4.7	4.7
Pinkham Notch.....	30	0.700	0.260	0.170	2.6	4.9
Tripyramid.........	72	1.450	0.680	0.292	13.1	4.5
Franconia Notch....	old	1.450	0.680	0.435	13.1	4.2
Pinkham Notch.....	old	1.450	1.350	0.300	14.4	4.1
Tripyramid.........	old	0.800	1.100	0.342	13.2	4.3
2-4″ LAYER						
Franconia Notch....	9	0.250	0.070	0.110	4.8	4.9
Pinkham Notch.....	30	*	*	*	*	*
Tripyramid.........	72	0.500	0.130	0.130	10.1	4.9
Franconia Notch....	old	0.050	0.120	0.115	7.1	4.8
Tripyramid.........	old	0.500	0.220	0.170	11.0	4.7

* Samples not taken due to extreme rockiness.

istics of the soils on which the sampled vegetation was growing. They also give general information on probable trends with time. The samples from the surrounding mature forests (estimated to be over 200 yrs. old) are assumed to represent a possible final condition.

Since organic matter values were derived from a wet-digestion method, amounts probably run somewhat lower, because of incomplete oxidation, than total organic matter. The very low value for the 30-year-old Pinkham slide is probably not significant in terms of change with time. It does indicate, however, that successful revegetation by pioneer tree species is not dependent on appreciable organic matter content, since a good stand was growing on the site. In 72 years a full build-up of organic matter in the top 4 in. to the level of the surrounding forests is possible, as indicated by the Tripyramid North values. No tests for total nitrogen were run, but it may be assumed that these amounts would be proportional to amounts of organic matter.

Exchangeable calcium, magnesium, and potassium all show consistent build-up with time from low levels. In 72 years they have reached the general magnitude shown by the soils of the surrounding forest.

The pH values are consistently acid on all soils tested, all lying in the range 4-5. A very slight increase in acidity with time is shown in the top 2 in. layer, but it is so slight that it is fair to conclude that this factor plays no significant part in the change from pioneer to climax herbaceous species.

Available phosphorus was tested for by putting a fixed weight of soil into an HCl-H_2SO_4 solution for a specified length of time. Results thus derived from an equilibrium reaction are probably not dependable for quantitative comparisons, and are therefore not reported.

Discussion

Slide successions in the White Mountains share the four most important pioneer tree species—paper and yellow birch, pin cherry, and trembling aspen—with successions following fire, lumbering, and windthrow. But proportions are not the same and there are other differences. In slide revegetation herbaceous stages are brief and minor and shrubby species of little consequence. This is in marked contrast to the situation following either windthrow or lumbering, where shrubs (esp. *Rubus idaeus* and the almost shrubby *Acer spicatum*) may dominate the scene for some time, delaying restocking by tree species. In such cases the shrub species benefit from having seed and roots preserved undisturbed in the organic soil. Pin cherry is usually far more numerous following windthrow, lumbering, and light fires than in slide successions for the same reason: its seed is banked in the duff, which is preserved in the former three situations but not in slides.

Wherever adequate seed sources are left, spruce and fir come in as a slowly developing understory, which gradually increases in importance with time, and is destined to become the climax canopy at higher altitudes. Such adequate seed sources are least likely to be left following widespread clear-cutting or severe fire (or both—a frequent occurrence in the White Mountains prior to the establishment of the White Mountain National Forest).

Slide revegetation varies tremendously with respect to speed. Upper bare rock, bared till, and slide talus may remain largely free of vegetative cover for more than 100 years—hence the scars so conspicuous in the region. But general observation indicates that all such areas, except the steepest and sheerest ledges (which may persist almost indefinitely as cliffs), become completely revegetated in time. Successions on bared rock, till, and slide talus, dealt with in general fashion only in this paper, are examples of true primary succession.

Lower, less steep, and more protected habitats, and especially residual and deposit areas, may revegetate rapidly. In the early stages (the first 50 years or so) the light green pioneer hardwood growth of such sections contrasts conspicuously with the dark green of the predominantly spruce-fir forests at higher altitudes.

Succession on deposit areas, representing slide sites capable of rapid revegetation, are technically not purely primary, since some organic matter, plant fragments and seeds are mixed with the mineral material. The pattern of succession is evident from the data and is given in summary form in Fig. 7. This figure, based on calculated importance values, is a generalization for the 1500-3000 ft. altitude range. The thickness of each bar for the tree species is to scale and represents the importance value. The values for the 9-year-old group, depending on quadrat data, are not strictly the same as those of other age groups, which derive from quarter data. But to indicate general trends, they are considered roughly comparable. There are no importance data for pioneer shrubs, nor for pioneer and terminal herbs; these three groups have thickness in the diagram derived only from frequency values and educated guesses of relative cover. They cannot therefore be related to the other bars in an exact quantitative sense. The time scale is approximate, and in specific cases might be shifted either way.

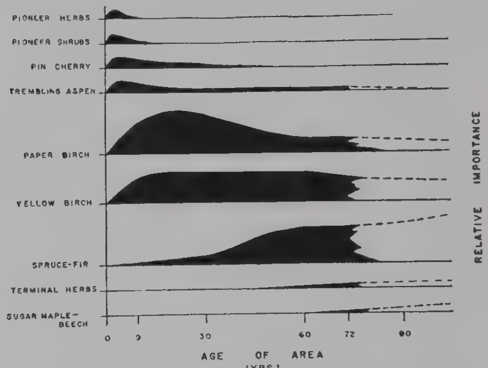


FIG. 7. Summary diagram: change with time of relative importance of vegetation on deposit areas of slides. Bars for tree species are based on importance values from quarters data (or, in the case of 9-year-old area, from quadrat data). Bars for herbs and shrubs represent estimates of importance in a general sense, based largely on frequence data from quadrats.

Paper and yellow birch, pin cherry, and trembling aspen begin immediately and may produce a thicket rapidly. In such pioneer stands the two birches show by far the greatest numbers, but are exceeded in height growth by both pin cherry and aspen. Pin cherry has died out of the stands by age 60 years, and aspen begins to drop out at this age. Paper birch importance shows marked reduction by 72 years, yellow birch is somewhat reduced, and red spruce and fir have become steadily more important. Development toward a climax is already well advanced at this age. At least at the higher altitudes such a climax is destined to be dominated by spruce or fir or both. Some quantitative idea of the possible composition of these climax spruce-fir forests can be obtained from Oosting and Billings' (1951) paper, which gives data for four virgin spruce-fir stands in the White Mountains, all at altitudes from 2500 ft. to 2750 ft. Their ecomposite phytographs show dominance by red spruce (very high basal area and variety of size classes) and balsam fir (slightly higher density though much lower basal area and size-class variety), with the two birches making up a small but significant part of the community, and mountain maple and mountain ash occurring as subordinate layer species.

Little progress toward a possible lower altitude climax of sugar maple-beech-yellow birch, probably the commonest northern hardwood type on lower slopes in the region, was shown in 72 years.

Throughout this paper the terms "climax," and "terminal" have been used frequently. These terms as here used are not intended to imply a fixed, single, and final condition, but rather a late-stage condition which can and does vary locally and which is only relatively stable when compared to the fast-changing pioneer stages. The composition of mature White Mountain forests has been profoundly affected in the past by lumbering, fire, windthrow, and very likely insect pests and diseases. Windthrow, especially severe at higher altitudes, must be reckoned as an important and almost constant disturbing agent, indeed a natural part of the climax situation. Paper birch, especially the higher altitude *cordifolia* variety, has suffered widespread mortality in the White Mountains from causes not yet understood. And the beech scale-Nectria disease is at present an increasing factor affecting the beech at lower altitudes. The climax condition, then, must be regarded as a varying and changeable one, stable only in a relative sense when compared to pioneer stages.

SUMMARY

1. Revegetation was studied on 29 landslides in the White Mountains of New Hampshire. Landslide habitats were classified into: (a) bare cliffs and ledges, (b) rock debris or slide talus deposits, (c) areas of erosion in glacial till, (d) residual areas, (e) areas of deposit. Revegetation is very slow on the first two, may be slow or rapid on the third, and is usually rapid on the last two types.

2. General commonness of species on all slide habitats of all ages is reflected by presence percentage values. Such species as *Betula papyrifera, Prunus pensylvanica, Rubus idaeus, Aster acuminatus,* and *Anaphalis margaritacea* showed especially high values.

3. Vegetation was quantitatively sampled on deposit areas of a chronoseries of slides 9, 19, 30, 60, and 72 years old. Relative values and their summation importance values were compared for tree species to show changes with time and altitude.

4. Herb and shrub stages are comparatively minor on deposit areas. Paper and yellow birch, pin cherry, and trembling aspen begin immediately and rapidly develop a thicket. In the dominant canopy there is a gradual shift from pioneer species. By 72 years pin cherry has disappeared, aspen is dropping out, paper birch is much reduced, and spruce and fir are correspondingly increased in relative importance. Development at

higher altitudes toward spruce, fir, or spruce-fir climax is well advanced by this age. At lower altitudes little or no invasion of beech was noted in the 72 years of the chronoseries.

5. Frequency data show a progression on deposit areas from a pioneer type herb spectrum through a stage of paucity of herb species to a terminal type herb spectrum. At 72 years the latter is quite similar to that of surrounding forests.

6. Analysis of stand composition at different altitudes on the 9-year-old slide showed: (a) decreased growth rate at higher altitudes for all species (b) greater relative abundance of paper birch at higher altitudes and yellow birch at lower altitudes (c) the following height-growth ranking, at all altitudes, of the four commonest tree species: pin cherry > aspen > paper birch > yellow birch.

7. Soil analyses of the surface 4 inches on the 9-, 30-, and 72-year-old deposit areas showed a build-up of organic matter and exchangeable calcium, magnesium, and potassium to levels comparable to those of surrounding forests. The pH values showed only very slight increase in acidity in the surface 2 inches.

REFERENCES

Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology **37**: 451-460.

———, **J. T. Curtis and B. W. Hale.** 1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology **34**: 741-757.

Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology **32**: 476-496.

Ellison, L. and J. E. Coaldrake. 1954. Soil mantle movement in relation to forest clearing in southeastern Queensland. Ecology **35**: 380-388.

Flaccus, E. 1958a. Landslides and their revegetation in the White Mountains of New Hampshire. Ph.D. dissertation, Duke University, Durham. 186 pp.

———. 1958b. White Mountain landslides. Appalachia **32**: 175-191.

Fernald, M. L. 1950. Gray's Manual of Botany 8th edition. American Book Co.

Hodgdon, A. R. and F. L. Steele. 1958. The woody plants of New Hampshire. Agricultural Experiment Station, University of N.H. Station Bull. **447**.

Japanese Government Forest Experiment Station. 1956. A study of 1954 flood. Meguro, Tokyo (in Japanese, with English résumé).

Keever, Katherine. 1950. Causes of succession on old fields of the Piedmont, North Carolina. Ecological Monog. **20**: 229-250.

Lakela, Olga. 1939. A floristic study of a developing plant community on Minnesota Point, Minn. Ecology **20**: 544-552.

Langenheim, Jean H. 1956. Plant succession on a subalpine earthflow in Colorado. Ecology **37**: 301-317.

Leisman, G. A. 1957. A vegetation and soil chronosequence on the Mesabi Iron Range spoil banks, Minnesota. Ecological Monog. **27**: 221-245.

Olson, J. S. 1958. Rates of succession and soil changes in southern Lake Michigan sand dunes. Bot. Gaz. **119**: 125-170.

Oosting, H. J. and W. D. Billings. 1951. A comparison of virgin spruce-fir forest in the northern and southern Appalachian system. Ecology **32**: 84-103.

Rowe, J. S. 1956. Uses of undergrowth plant species in forestry. Ecology **37**: 461-473.

Westveld, M. et al. 1956. Natural forest zones of New England (prepared with committee of Society of American Foresters). Jour. Forestry **54**: 332-338.

THE CLASSIFICATION OF LOWLAND SWAMP COMMUNITIES IN NORTHEASTERN PAPUA

B. W. Taylor
Land Research and Regional Survey Section, C.S.I.R.O., Canberra, Australia

INTRODUCTION

Two areas, both approximately 5,000 km^2, in northeastern Papua were studied by a natural resources survey team of the Land Research Section of the Commonwealth Scientific and Industrial Research Organization. Detailed descriptions of these areas are now being prepared for publication.

Climatically, northeastern Papua is part of the wet tropics with a mean temperature at sea-level of 27°C and a mean annual rainfall ranging from 2,800 mm to over 3,600 mm. There is a regular "dry" season but in all places the average rainfall of the driest month is more than 100 mm. Typically a wide alluvial plain extends from the high central ranges to the sea but it is broken in many places by volcanic ranges and cones. This alluvial plain is largely covered by rainforest and numerous secondary communities, including some grasslands, and there are several extensive areas and numerous smaller areas of swamps. The object of this paper is to describe the climax swamp commu-

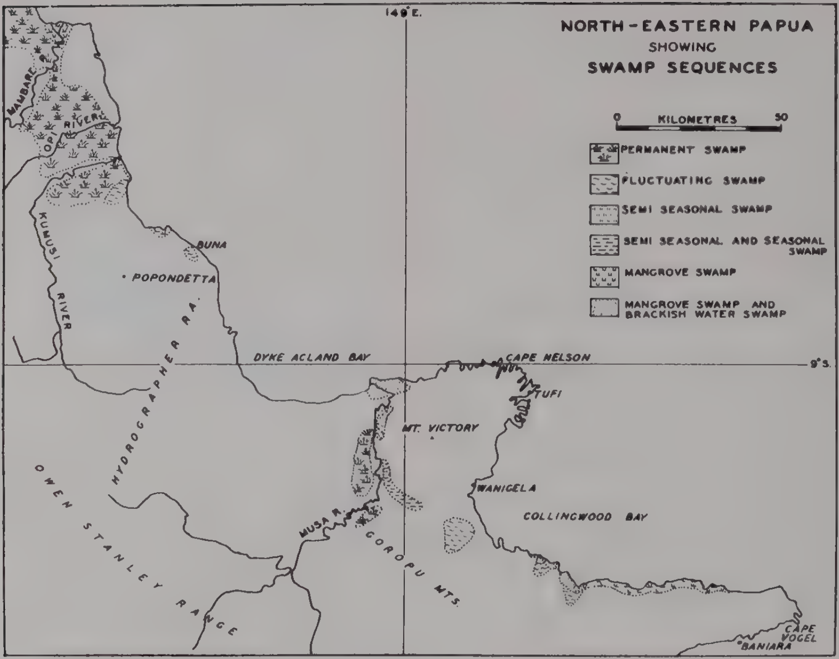

NORTH-EASTERN PAPUA
SHOWING
SWAMP SEQUENCES
0 KILOMETRES 50
PERMANENT SWAMP
FLUCTUATING SWAMP
SEMI SEASONAL SWAMP
SEMI SEASONAL AND SEASONAL SWAMP
MANGROVE SWAMP
MANGROVE SWAMP AND BRACKISH WATER SWAMP
148°E.
9°S.
MAMBARE R.
OPI RIVER
KUMUSI RIVER
BUNA
POPONDETTA
HYDROGRAPHER RA.
DYKE ACLAND BAY
CAPE NELSON
TUFI
MT. VICTORY
WANIGELA
COLLINGWOOD BAY
MUSA R.
GOROPU MTS.
OWEN STANLEY RANGE
CAPE VOGEL
BANIARA

Fig. 1. Map of northeastern Papua.

nities together with their ecological relationships, and to arrange them into a system of classification that permits comparison with vegetation types in other tropical areas.

Different systems for tropical vegetation descripion and classification have been used by various authors including Schimper (1903), Shantz and Marbut (1923), Burtt-Davy (1936), Champion (1936), and Beard (1944, 1955). These systems were examined but none was found to be entirely satisfactory although the system evolved by Beard facilitated the classification of many of the types encountered. Since the author felt that little was to be gained by the use of a different system of classification in each region of the tropics, Beard's system and terminology were tentatively adopted. This system proposed that climax vegetation be classified floristically into associations, structually into formations, and that the formations be arranged on an environmental basis into formation series. However the study of the swamp communities described in this paper, besides making the erection of new formations necessary, indicated the dangers of oversimplification inherent in Beard's environmental classification of formations.

Grateful thanks are due to other members of the survey team, particularly Mr. H. A. Haantjens who provided most of the information on soils, and to Dr. R. D. Hoogland and Mr. J. Saunders for the collection and identification of plant specimens.

Description

Beard recognized only two groups of climax swamp communities, the swamp formation series and the seasonal swamp formation series. In northeastern Papua, eight groups of swamp communities were recognized. These are described as environmental sequences which are sequences actually encountered in the field but do not necessarily correspond to a formation series. The geographical distribution of these sequences is shown in Fig. 1. The formation name of different stages of a sequence follows Beard's usage whenever it is felt that the structural characteristics of the communities described are essentially similar. It should be noted that one formation can occur in different environmental sequences.

The main factors differentiating the various swamp sequences are the type of water, whether fresh, salt or brackish, and the depth, duration, and frequency of flooding. Apart from the environmental sequences listed below there are also several rainforest communities found in swampy areas.

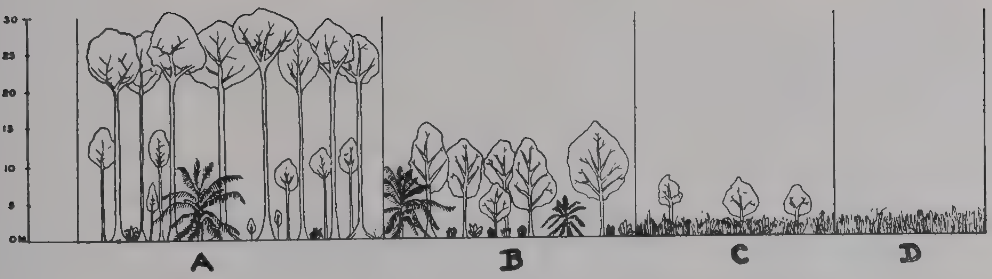


FIG. 2. Permanent swamp sequence.
A. Swamp forest
B. Swamp woodland
C. Swamp savanna
D. Herbaceous swamp (sedge)

A. Fresh water swamps
  1. Permanent swamp sequence
    (a) Swamp forest
    (b) Swamp woodland
    (c) Swamp savanna
    (d) Herbaceous swamp (sedge)
  2. Fluctuating swamp sequence
    (a) Seasonal swamp forest
    (b) Open seasonal swamp forest
    (c) Seasonal swamp woodland
    (d) Herbaceous swamp (tall grass)
  3. Semi-seasonal swamp sequence
    (a) Seasonal swamp forest
    (b) Open seasonal swamp forest
    (c) Seasonal swamp woodland
    (d) Herbaceous swamp (sedge)
  4. Seasonal swamp sequence
B. Salt water swamps
  1. Tidal mangrove sequence
    (a) Herbaceous swamp (short grass)
    (a) Mangrove forest
    (b) Mangrove woodland
  2. Mangrove marsh sequence
    (a) Mangrove woodland
    (b) Mangrove thicket
C. Brackish water swamps
  1. Brackish water sequence
    (a) Mangrove-fern savanna
    (b) Fern-tall tree savanna
  2. Estuarine sequence
    (a) Swamp thicket

A. Fresh Water Swamps

1. Permanent swamp sequence

The permanent swamp sequence covers the major part of the very extensive (800 km^2) swamps between the lower reaches of the Mambare and Kumusi Rivers. Elsewhere, there are only small areas of this sequence, the largest being near the west bank of the Lower Musa River. The sequence occurs on flat alluvium at low elevations. The soils are generally peat, often of great depth, but some swamp forest communities occur on mineral soils. These soils never dry out and even during the dry season the water table is at, or very near, the soil surface. Four structural types (Fig. 2) have been recognized in this sequence.

(*a*) *Swamp forest.*—This is a two-tree-layered evergreen forest community with the upper layer forming a canopy from 15-35 m high. The lower tree layer and the shrub and ground layers are relatively sparse. Buttressing, prop-roots and pneumataphores commonly occur but lianes and epiphytes are rare. The floristic composition of the canopy layer varies considerably. In some areas, a single species, *Campnosperma auriculata* (Bl.) Hook. f., predominates, whereas in others the layer is of mixed composition. The lower tree layer is composed of small individuals of species present in the canopy layer and of smaller growing species notably sago palm, *Metroxylon sagu* Rottb. The ground flora consists of scattered tufts of sedges and grasses, notably *Thoracostachyum sumatranum* (Miq.) Kurz.

(*b*) *Swamp woodland.*—This is a woodland community of evergreen trees with short boles, and communities classed in this group have a range of different structures. At one extreme, the canopy is dense and fairly tall (up to 20 m) and there is a sparse lower story of trees and a sparse ground layer. At the other extreme, there is only a single layer of trees which may be as low as 8m, which is relatively open, and a dense ground layer 1-3 m high. Communities intermediate in height between these extremes may have a well-developed lower layer of trees, principally of the sago palm, *Metroxylon sagu*. The number of species in the canopy layer of these swamp woodland communi-

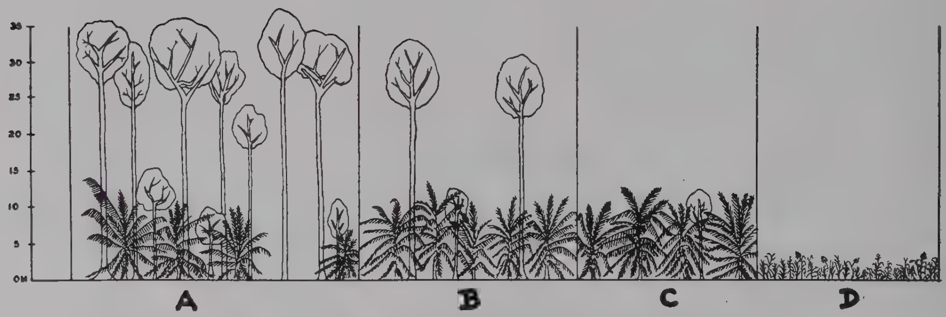


Fig. 3. Fluctuating swamp sequence.
A. Seasonal swamp forest
B. Open seasonal swamp forest
C. Seasonal swamp woodland
D. Herbaceous swamp (tall grass)

ties is less than in the swamp forest communities, with *Syzygium* sp. and *Campnosperma auriculata* predominating.

(*c*) *Swamp savanna.*—This community has a very dense and tall ground layer, approximating 3 m high with scattered trees. The trees vary greatly in height, from 5 to 12 m, and in density, but in any one stand tree height is relatively uniform. *Syzgium* sp. and *Campnosperma auriculata* were both recorded as common in this community. The ground layer is very similar to the herbaceous swamp communities and is dominated by *Thoracostachyum sumatranum* and *Hanguana malayana* (Jack) Merr.

No mention is made of any community of a similar structure by Beard (1955), who has designated swamp thicket as the intermediate community between swamp woodland and herbaceous swamp. Beard notes that his swamp thicket is a river-bank type; and in a personal communication states that, "the swamp savanna which you describe may possibly be found to be the correct member of the series in tropical America also, once we have more information." The Trinidad swamp, termed palm swamp by Beard (1944), is of somewhat similar structure but Beard (1955) states that it is possibly a fire climax and has been provisionally dropped from his classification.

(*d*) *Herbaceous swamp* (*sedge*).—This community has an extremely dense ground layer consisting of leaves and stems 2-4 m high. Occasional twining plants bind this mass together, the most conspicuous of these being a pitcher plant, *Nepenthes* sp. Usually *Thoracostachyum sumatranum* and *Hanguana malayana* occur as codominants but in an area of herbaceous swamp on Cape Vogel both these species occur in large pure stands. A few species of Cyperaceae and some grasses may occur, but the latter are rare.

The factors controlling the occurrence of an individual stage in this sequence have not been fully determined. All had a water table at or near the soil surface when visited during the dry season. The slopes between different stages were so gradual that it was impossible to determine their direction or to evaluate the relative height and drainage status of different stages. However, it was observed that herbaceous swamp occurred on peat deeper than the depth of sampling, 2 m, and that taller stages occurred in areas without peat or with shallower peat.

The various stages are undoubtedly climax. Although most of the surrounding country is fairly densely populated, the swamps are uninhabited. The only population in the Kumusi-Mambare swamp is centered in a few small villages along the levee banks of the main rivers. Villagers never enter the swamps surrounding these levee banks since travel as extremely difficult.

2. *Fluctuating swamp sequence*

Scattered throughout the alluvial lowlands are numerous small patches of swamp with water tables that fluctuate at frequent intervals. These patches may be up to 10 km^2 in extent but are generally much smaller. This sequence is found only on mineral soils. The sites are always fed by streams which regularly flood the area. After rains, drainage from such sites is relatively rapid, but the soil is not subject to desiccation between the frequent floodings. In one site, the regular backing up of a small stream by high tide caused an area of this sequence to be flooded by 30 cms of fresh water but at low tide the water table was below the surface. Four stages have been recognized in this sequence, Fig. 3.

There is no sharp change between the first three stages in the sequence, nor between seasonal swamp forest and rainforest. There is however a very abrupt change between seasonal swamp woodland and the herbaceous swamp.

(*a*) *Seasonal swamp forest.*—This two-storied forest has an upper uniform canopy layer of 25-35 m height below which there is a dense layer, predominantly of sago palms. The layer of tall trees is composed of many species that are also present in rainforest communities on swampy sites. The most important of these species of *Bischofia javanica* Bl., which may constitute 50 per cent of the trees, other common species being *Palaquium* sp., *Terminalia* sp., and *Alstonia scholaris* R. Br.

(*b*) *Open seasonal swamp forest.*—This community which is relatively extensive, represents a transition stage between seasonal swamp forest and seasonal swamp woodland. It has a closed canopy 10 m high identical with seasonal swamp woodland, over which tower emergent trees. These emergent trees, which are approximately 30 m in height, belong to species present in the dominant layer of seasonal swamp forest and vary in density from rare scattered trees to an almost closed canopy.

(*c*) *Seasonal swamp woodland.*—The stage consists of a single, dense layer made up almost entirely of sago palms, *Metroxylon sagu*, 6-12 m in height. Dicotyledonous trees do occur but are extremely rare. The spreading fronds of the sago palms reach almost to the ground which in many cases is covered by fallen fronds. The shrub and ground layers are absent.

(*d*) *Herbaceous swamp* (*tall grass*).—This is the last stage in the permanent swamp sequence. It is composed predominantly of the grass *Phragmites karka* (Retz.) Steud., 3-4 high, but many other species of tall grass are present in many stands as well as twining plants and small trees to 5 m high.

The factors controlling the occurrence of individual stages in this sequence appear to be the depth and period of flooding. Stages 1 to 3 occur in many sites with Stage 3, seasonal swamp woodland, in the lowest lying area. Herbaceous swamp (tall grass) is rare in this sequence and occurs only in association with other stages of the sequence on sandy soils where, although floodings are frequent, there are also short periods where the soil dries out to some depth. In such sites, herbaceous swamp dominated by *Phragmites karka* is a true climax, although an almost identical community can also occur as a pioneer stage in a succession following flooding.

3. *Semi-seasonal swamp sequence*

This sequence was seen only along the east bank of the Lower Musa River, near the lower slopes of a 2,000 m volcano, Mt. Victory. The swamps are on very low-lying areas but are partly seasonal due to the relatively small amount of water draining into them from Mt. Victory during the dry season. Although they are close to the Musa River, drainage is slow and the lower-lying areas are permanently inundated but progressively less frequent in taller stages of the sequence.

Apart from the herbaceous swamp stage which is identical in structure and floristics with the herbaceous swamp of the permanent swamp sequence and occurs in a very similar environment, the sequence is most like the fluctuating swamp sequence, differing mainly in that the sago palm is rare and is replaced by another tall monocotyledonous plant, *Pandanus* sp., a "screw pine" that is somewhat smaller in height, about 6-8 m.

4. *Seasonal swamp sequence*

Between the lower slopes of Mt. Victory and the alluvial plain flanking the Goropu Mountains is a low-lying area of swamp into which drain many streams from both regions. However, no stream drains this area of swamp, and excess water seeps slowly into the Musa River. Water table fluctuations in this region are mainly seasonal or semi-seasonal, with small areas near the mouths of streams with a more frequent fluctuation of level. These swamps are formed solely on mineral soils and the more poorly drained areas have small permanent lakes in which are growing various aquatic communities, *Myriophyllum* sp., *Lemna* sp., and *Nymphaea* spp. predominating.

Surrounding these water pools is an herbaceous swamp (short grass) that consists of an almost pure stand of a single glass species, probably *Saccharum* sp., but the species was not seen in flower or fruit. This grass is less than 1 m high and the water table, even during the dry season, is within 30 cms of the soil surface. Further development of the sequence is indicated by the presence of a few scattered trees, predominantly *Neonauclea* sp., and then there is a rapid change to seasonal forest, rather similar to the changeover in the Aripo savanna (Beard 1953: 205). This sequence does not correspond to the seasonal swamp formation series of Beard (1955), due in part to the relatively high rainfall experienced in the dry season. This sequence is also interrupted after the herbaceous swamp (short grass) stage and is replaced by stages in the semi-seasonal or the fluctuating swamp series near the entry point of many streams bringing water into the swamp.

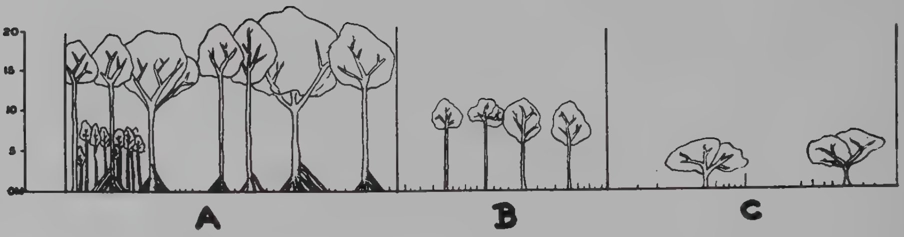


Fig. 4. Mangrove communities.
A. Mangrove forest
B. Mangrove woodland
C. Mangrove thicket

B. Salt Water Swamps

1. Tidal mangrove sequence

Small patches of mangroves rarely more than ½ mile wide occur along the coast of northeastern Papua. Within these patches, two sequences were recognized. The most common is a simple tidal sequence occurring between rainforest and the sea. The rainforest in this coastal area was originally dominated by many species including *Intsia bijuga* (Colebr.) O.K., but is now largely replaced by young stages of garden regrowth. Generally, the boundary between rainforest and mangrove forest is very sharp and marked by a line of *Intsia bijuga* trees. These are succeeded by successive communities of mangrove forest which are finally replaced by a mangrove woodland community near the open sea. Each succeeding community occurs in sites with successively longer period of tidal inundation.

The mangrove forests (Fig. 4) are similar in structure to swamp forest as described by Beard (1955). These communities are most frequently composed of a single tree layer, 15-25 m in height, of evergreen trees commonly with prop roots and pneumataphores, but the frequency of these organs varies with different communities. There is occasionally a dense second layer which may be either small trees or shrubs. The ground layer is very sparse and consists solely of seedlings of mangrove species. Three floristic communities of mangrove forest have been recognized and these are arranged in well-defined bands. Proceeding from rainforest, a narrow zone dominated by *Heritiera littoralis* Dryand. is encountered, then a broad zone dominated by *Bruguiera gymnorrhiza* (L.) Lamk, and then another broad zone of *Rhizophora mucronata* Lam. The single layered mangrove woodland is dominated by *Ceriops tagal* (Perri) C. B. Rob. In addition to these four dominant species, a small number of other species occur. Any or all of the mangrove species may occur as scattered individuals in the various communities, although the dominant species usually makes up over 50 per cent of the number of individual species, and there are rather sharp transitions between the various communities.

2. Mangrove marsh sequence

In addition to the normal tidal sequence, there are many small patches of a second sequence in sites surrounded by mangrove forest. In this sequence, there is a range in structure from woodland to bare ground (Fig. 4) but only one species, *Avicennia alba* Bl. cf. *marina* occurs. On the fringes of the area, the community consists of a dense single layered mangrove woodland 12 m in height and changes gradually to a mangrove thicket 6 m in height. At this stage, the sequence is continued by a gradual thinning of the canopy without change in height, until the point is reached where a few widely scattered trees, 6 m high, are surrounded by an area of swampy soil completely devoid of vegetation. It is suggested that the stages in this sequence are determined by the salt concentration present in the soil.

C. Brackish Water Swamps

Two sequences of brackish water swamps are described. The first, the normal brackish water sequence is found in a transition zone where fresh water swamps are inland from mangrove communities. The second type, the estuarine sequence, occurs near the mouths of rivers and creeks where sea water and fresh water are interchanged by tides and river floods.

1. Brackish swamp sequence

Where mangrove forest and some fresh water swamp communities meet, there is a transition area generally only a few hundred meters in width but divided into two sharply defined stages (Fig. 5). Approaching from the mangrove forest, the first stage is a mangrove-fern savanna. This has scattered trees, 6-10 m in height, predominantly *Avicennia alba* cf. *marina* and *Bruguiera gymnor-*

rhiza, and a dense ground layer of ferns, about 1 m in height. The savanna community includes small patches of mangrove woodland also dominated by *Avicennia alba* cf. *marina* and *Bruguiera gymnorrhiza* but with much less dense ground layer. This community is apparently the intermediate in the transition to mangrove forest.

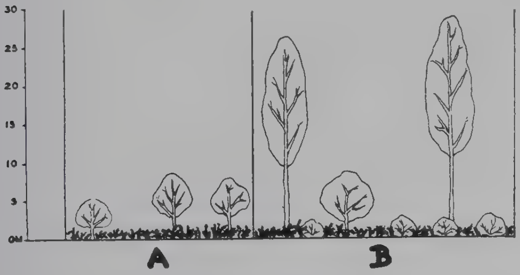


FIG. 5. Brackish water sequence.
A. Mangrove savanna
B. Fern-tall tree savanna

The second stage is a fern-tall tree savanna with scattered tall trees up to 30 m high. These trees belong to very few species, *Parinari corymbosun* (Bl.) Mig. predominating, all of which are present in the swampier types of rainforest. A few smaller trees occur, including *Hibiscus tiliaceus* L. and *Dolichandrone spathacea* (L.f.) K. Sch. The ground layer, 1 m in height, consists of a mass of ferns, *Acrostichum speciosum* Thunb. predominating, and a few scattered grasses. In some areas, this ground layer is partly replaced by scattered bushes 2-3 m high of *Acanthus ilicifolius* L. which make up 50 per cent of the ground cover.

The transition between these two zones is sharp, as is the transition between the fern-tall tree savanna and the fluctuating swamp series. When the sequence borders a swampy type of rainforest, however, the transition is gradual and is accompanied by a gradual increase in density of the tall trees and a lessening in density of the ground layer.

2. *Estuarine sequence*

Most of the rivers reaching the sea in northeastern Papua have well-defined levee banks, supporting tall rainforest, along the greater part of their length. However, mangrove forest identical with communities of the normal tidal sequence may occur and a transition between these two types is rare, the only community noted being occasional stands of swamp thicket consisting of a pure stand of the palm *Nypa fruticans* Wurmb. This community is very similar to the sago com- 7 m. It grows on areas which may be continually inundated or only drained for short periods, and it is probably that the water changes from pure fresh water to pure sea water at frequent intervals. The largest stand of *Nypa fruticans* seen was less than 50 hectares in extent and most stands were merely thin strips only a few meters in width along small rivers. However, this same community covers very large areas in western Papua (McAdam 1952).

D. Rainforest Communities on Swampy Sites

Many rainforest communities occur on sites subject to inundation. These are three-tree-layered evergreen forests identical in structure to rainforest as described by Beard. The intergrading of the various rainforest communities is in the nature of a continuum but due to major differences in composition they can be conveniently divided into associations in the manner described by Beard. These associations can be arranged in two environmental sequences that occur under different conditions of inundation, but both sequences lead up to a mixed rainforest community, with a preponderance of *Pometia pinnata* Forst., on sites where inundation is only slight. This community grades slowly into rainforest on well-drained sites where no one species is even prominent.

The first sequence of rainforest on swampy soils is continuous with the permanent swamp sequence. The transition between the two-tree-layered swamp forest and rainforest is, however, very sharp, without any corresponding sharp change in environment. The only intermediate stage noted was the occurrence, in one small stand with a typical swamp forest structure, of many trees belonging to species typically found as dominants in swampy rainforest.

The first member of this sequence is a community with a strong tendency to single species dominance, *Palaquium* sp. making up 50 per cent or more of the individual trees in the dominant layer of any one stand. Further, this species due to its large size, over 45 m in height, plays an even greater part than this figure suggests, and accounts for over 70 per cent of the commercial timber present in any one stand. There are, however, many other species present in the *Palaquium* sp. association, some 30 species being actually recorded from its dominant layer and doubtless this figure is far from complete. The *Palaquium* sp. association changes gradually into the *Pometia pinnata-Dillenia quercifolia-Palaquium* sp. association and this then changes gradually into the *Pomentia pinnata-Dillenia quercifolia* association. In these associations, the named species make up approximately 50 per cent of the trees in the dominant layer, the remaining individuals belonging to a large number of different species. The full sequence occurs just south of the Kumusi-Mambare swamps with the different communities succeeding each other as the distance from the true swamp forests becomes greater. The slope of this area was almost imperceptible with a corresponding gradual change in drainage conditions.

The second sequence of swampy rainforest communities is continuous with seasonal swamp forest of both the fluctuating and semi-seasonal swamp sequences. Two associations are encountered, the *Bischofia javanica* association and the *Terminalia* sp. association, but the composition of both communities is very mixed, with the predominant species rarely exceeding 20 per cent of the dominant layer in any one stand.

Discussion

In his 1944 paper, Beard proposed a system for the classification of vegetation in tropical America. Beard's system has been followed by recent workers in that region and their results have been incorporated in Beard's 1955 paper. This system, although designed purely for tropical America, appears to be the most suitable system in the literature to show the successional and other mutual relationship of communities in Papua, and at the same time permits a comparison of vegetation types on a wide basis. An examination of the swamp communities described in this paper, however, brings forward several principles that the author believes are of more than local importance.

Floristic groupings, while of the utmost value for the understanding of local variations in vegetation, are of little use in comparing vegetation on a world basis. Physiognomic units however, offer a basis on which vegetation of widely separated regions of the tropics can be compared and contrasted. It is frequently found that stands of vegetation with completely different floristic composition may have essentially similar structure and life form as the result of an interaction of a similar complex of environmental factors. One difficulty is the recognition and separation of those factors in the structure of a community which are a structural expression of floristic composition and those which are true indicators of a structural variation in response to the physical environment. In particular, palms could be treated as a distinct life form or regarded merely as a floristic group. Beard used palms as a major diagnostic character in his 1944 paper but in 1955 stated that it does not appear that palms are as important a diagnostic feature as previously suggested, and that there are palm-dominated variants of rainforest, seasonal forest, savanna and many other communities. Similar variants also occur in Papua. In addition to palms, many species of screw pines are sometimes found locally prominent in various communities including rainforest. These screw pines also are monocotyledonous and belong to the family Pandanaceae, characteristically found in the Old World tropics and absent from tropical America. These species have a characteristic life form with less variation than the life form of palms, and have equal justification to be recognized as a diagnostic feature in a structural classification. This, of course, means that formations so defined would be strictly limited to the Old World. The alternative seems to be either the grouping together of palms and Pandanacea as a diagnostic feature, and possibly with floristic groups of similar appearance, *e.g.* Cycadaceae and tree ferns, or in treating them as floristic groups important in a floristic classification of a single botanical region, but regarded as trees in a structural classification which should have a wider application. This latter course seems advisable on present evidence until fresh work can show that these life forms are indications of environment transcending floristic boundaries as do other structural types.

The third level of Beard's classification is the grouping of formations into a formation series, such series consisting of a number of stages between the optimum and the most adverse. This concept is extremely useful and facilitates the description of a continuous environmental sequence of communities and their inter-relationships. The weakness of the concept is that it is not sufficiently stressed that the series arbitrarily selected by Beard does not necessarily coincide with environmental sequences encountered, nor is sufficient emphasis placed in the inter-relationship between stages in different series.

Some of the complex inter-relationships to be expected can be illustrated from the swamp communities already described. A particular example of center of radiation is the seasonal swamp woodland dominated by the sago palm. Apart from its environmental relationship with other members of the fluctuating swamp sequence, this community could equally be placed in a continuous environmental sequence next to fern-tall tree savanna, herbaceous swamp, swamp savanna, swamp woodland, seasonal swamp woodland, and open seasonal swamp forest (*Pandanus*). This environmental relationship occurs in a small region where the effects of variation in the numerous factors of climate and of the floristic factor are negligible. The community could equally well be jointed in environmental series where such factors as temperature, total rainfall, seasonal distribution of rainfall, etc. are varying. It follows that a very large number of structural types are theoretically possible, even within the tropics, but structural differences between many of them may be slight and they could well be distinguished by having a two-level structural system, such as formations and sub-formations suggested by Beadle and Costin (1952) for Australian vegetation. For example, all swamp woodland communities, formed under different regimes of temperature and flooding, could be grouped in one formation but separated into different sub-formations, ideally all woodland communities could be grouped together in one formation but this may lack practical significance.

When the various sequences are examined, it is readily seen that each stage represents a stepping down of structure, but it is noteworthy that this transition can be brought about in one of three ways. The first is by an abrupt change as in the fluctuating swamp sequence between seasonal swamp woodland and herbaceous swamp (tall grass). Here the change-over is no doubt due to the fact that the woodland consists of a pure stand of a single species. When the limit of this species is reached, the woodland disappears and is replaced by herbaceous swamp. The second method is the gradual reduction in height of a layer, with little or no reduction in density, until it merges with a lower layer or disappears. An example of this is the gradual transition from swamp forest to swamp woodland in the permanent swamp sequence. The third method is the gradual reduction in density of a layer until it disappears with little or no reduction in height. This is illustrated by the change in the fluctuating swamp series from seasonal swamp forest to seasonal swamp woodland with open seasonal swamp forest respresenting the immediate stage. A variation of this last method is found in the transition from rainforest to seasonal swamp forest, where there is a reduction in density of the middle tree layer until it disappears, and at the same time there is no appreciable change in height of the other two tree layers and only a slight change in their densities.

CONCLUSION

The system of classification evolved by Beard for the vegetation of tropical America, offers a basis for the classification of other tropical vegetation. However an examination of even the restricted range of vegetation types described in this paper shows that many modifications are necessary. It is likely that many of these changes are of general application, and examination of similar environments elsewhere in the tropics, including tropical American, may show the presence of allied structural forms.

Further series will undoubtedly need to be added to Beard's classification, other series subdivided, and some modifications to the formations placed within a series. It is felt that the brackish water sequence should be classed as a new series. Beard's existing swamp series should be split into two, the permanent swamp series and the mangrove series. A further series should be erected, the fluctuating swamp series to cover most stages of the fluctuating swamp sequence and semi-seasonal swamp sequence, and Beard's swamp series should be modified by replacing swamp thicket with swamp savanna. However, it must be continually stressed that these are merely arbitrary units into which it is convenient to divide the continuous variation of structural forms.

SUMMARY

The structure and floristic composition of eight environmental sequences of climax swamps, found on extensive alluvial plains in northeastern Papua, are described. Each sequence is divided into arbitrary structural stages and the factors controlling the occurrence of each sequence and of the various stages are discussed. The system of classification proposed by Beard for tropical America is adopted, but various suggestions are put forward to incorporate the particular communities described. Various other modifications of Beard's classification are suggested with the object of using this system throughout the tropics.

REFERENCES

Beadle, N. C. W., and A. B. Costin. 1952. Ecological classification and nomenclature. Proc. Linn. Soc. N.S.W. **77**: 61-82.

Beard, J. S. 1944. Climax vegetation in tropical America. Ecology **25**: 127-158.

———. 1955. The classification of tropical American vegetation types. Ecology **36**: 89-100.

Burtt-Davy, J. 1938. The classification of tropical woody vegetation types. Imp. For. Inst. Paper No. **13**, Oxford.

Champion, H. G. 1936. A preliminary survey of the forest types of India and Burma. Indian Forest Records (N. S.) Silviculture **1**, No. **1**, New Delhi.

Fanshawe, D. B. 1952. The vegetation of British Guiana. A preliminary review. Imp. For. Inst. Paper No. **29**, Oxford.

McAdam, J. B. 1952. Forestry in New Guinea. Papua and New Guinea. Scientific Soc. Ann. Rep. and Procs. pp. 41-61.

Schimper, A. F. W. 1903. Plant geography upon a physiological basis. Oxford.

Shantz, H. L., and C. F. Marbut. 1923. The vegetation and soils of Africa. Amer. Geog. Soc., Res. Series **13**: 1-242.

NOTES AND COMMENT

A NEW APPROACH TO THE STUDY OF MARINE BACTERIA IN GULF AND ATLANTIC WATERS[1]

Introduction

Just as soil bacteria are essential to the terrestrial life cycle, so evidently do marine life forms from minute diatoms to giant whales, directly or indirectly, depend on the activities of marine bacteria for their growth and development.

Essential to the life cycle of all marine flora and fauna are the heterotrophic and autotrophic bacteria that, from our observations, exist in nutrient waters by the millions in a cubic centimeter or single drop of sea or brackish inland water.

The seemingly inexhaustible oceanic meadows of photosynthetic algae and related bacteria merit further study because of the increasing need for conservation of marine life as a service to the sea food industry.

To start with, contemporary hypotheses suggest that there may be more and varied types of viable bacteria in sea and inland bay waters than may be isolated by present methods. In order therefore, to devise some new possible techniques for a more tenable study of marine bacterial flora, and to secure data on their numerical incidence, classification and biochemical activities, a wide range of water samples was taken at varying depths for a more detailed microbiological study.

Most of the samples were taken from the northern Florida, Atlantic coastal waters and the Gulf of Mexico, inland bays and estuarine salt waters, in the vicinity of Jacksonville, Neptune Beaches, Alligator Harbor and Ball Point, Panama City Gulf, and Long Beach, nearby St. Andrews Park inlet, Spanish Cove, and Panama City Bay. In addition, trips were made in commercial Mayport Shrimpers where varying water depth samples were taken from neritic pelagic waters rich in all manner of sea life.

Methods and Techniques

Slide Immersion

Ordinary wooden slide boxes were modified as traps to catch viable and non viable marine bacteria along with other plant and animal biota. The top and bottom of the slides were knocked out and painted. Slots were cut on the inner surface to fit the slides and were placed (a) horizontal (b) vertical and (c) tangential. The boxes were covered with plastic mesh screening and attached to the edges with thumb tacks for quick release. Lead sinkers were fixed to the boxes to steady them against the current and tide (Figure 1). The slides were kept in alcohol till ready for use.

The traps containing slides were immersed, by cord or wire joined to screw eyes, in Atlantic Ocean, Bay and Gulf waters at varying depths for periods of from 2 hours to 2 weeks. After immersion, the slides were air dried, stained with Gram's iodine or methylene blue, and examined with the oil immersion lens for morphological spore forming types, staining characteristics and numerical incidence. Hanging drop slides with dark field illumination were also prepared for motility data.

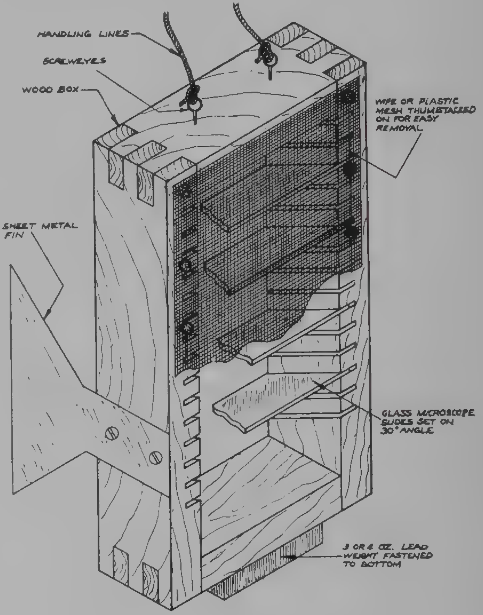

HANDLING LINES
SCREWEYES
WOOD BOX
WIRE OR PLASTIC MESH THUMBTACKED ON FOR EASY REMOVAL
SHEET METAL FIN
GLASS MICROSCOPE SLIDES SET ON 30° ANGLE
3 OR 4 OZ. LEAD WEIGHT FASTENED TO BOTTOM

Fig. 1. The bacterial trap slide box.

Frost Colony Slide Technique

Sterile slides were dipped in various differential Difco culture media made either with sterilized fresh or salt water. The coated slides were next inoculated while of liquid consistency at 40° C with 1⅒ cc of sea, gulf or bay water. The slides so cultured were incubated at 37° C for 8 hours when the colonies were read with a colony counter or low power microscope.

Frost Slide Culture Method

Sterile slides with roughened surfaces were dipped in various Difco differential media and placed in bacterial traps (Fig. 1) with exposure by immersion in Atlantic coastal, gulf and bay waters at different depths for from 10 minutes to 2 hours. One side of the slide was washed off with alcohol, while the other was stained with methylene blue 10% in alcohol and acetic acid and placed in the incubator at 37° C. Colonies were read with a Spencer colony counter and binocular dissecting microscope after 8 hours growth. Surprisingly enough, because of mechanical or electrical charge action, the film of medium on the slide was seldom washed off in spite of wind, current and tide. Colonies grew luxuriently and were readable after the 8 hour incubation.

Plate Count Using Standard Methods of Water and Milk Analysis

Difco culture media were made in 2 batches: (a) with fresh water (b) with local salt or brackish water. The media so made included Difco Nutrient agar, brilliant green bile medium, brilliant green agar, glycerine medium (for proteolysis), desoxycholate and Levine's EMB medium (for coliforms and gas formers), Czapok agar (for marine bacterial and fungal growth) and blood agar for possible pathogens. Petri dishes were initially sterilized with the hot air oven sterilizer at 160° C for one hour. Medium was prepared according to standard methods and Difco formulae, and autoclaved for 30 minutes at 15 to 20 pounds steam pressure per square inch at 120° C. Flasked salt and fresh water media were placed in a hot water bath till cooled to 40° C, poured into sterile Petri dishes and immediately inoculated with sample waters using pour plate tecnhique, (a) undiluted using 1/10 cc test water per plate for luxuriant growth, (b) dilutions of 1/10 and 1/100.

---

[1] We are indebted to Brian E. Michaels for taking the photographs, Figs. 2, 3, and 4.

The samples were taken (a) at the surface, (b) at 10 foot depths and (c) from the bottom. The salinities were recorded which varied from 1,030 to 1.031, while the temperatures ranged from 23.8 to 25° C, in gulf waters and 20° C in Atlantic waters. The plates were incubated at various room temperatures or at 37°C for 24 hours, when numerical classification and comparative colony counts were made. With presumptive identification and classification attempted, the different types of picked colonies were then inoculated into (a) gas tubes glucose, dextrose, mannitol and lactose (b) green bile (c) gelatin stabs (d) Kleger's iron slants (e) blood agar plates (f) Simmons' citrate medium.

Interpreting the 24-Hour Plates and 8-Hour Culture Slides

Colonies were divided for rough differentiation into (a) rough and smooth spreaders (b) large and small white mucoids (c) small translucent surface and subsurface colonies regarded as presumptive anaerobes (d) liquefiers of gelatin regarded as possible proteolytic enzyme producers (e) coliforms and *Aerobacter*, and (g) autoprophic bacteria including *Chlamydo bacteriales.*

Immersion slides were stained with Gram's iodine and tentatively classed as gram positive or negative, motile or non-motile, spirilla, bacilli, bacteria, spore bearers, molds or yeasts.

Using nutrient agar and various determinative media, 24-hour growth colonies were examined and counted in a Spencer counting chamber to secure comparative data from the following: (a) local salt water media (b) sterile water media (c) top compared with bottom samples of gulf and bay awters (d) brackish, turbid waters where the Secchi disc was visible at one yard or less (e) clear, transparent open gulf waters where the Secchi disc readings were 20 feet or better. Plate counts of the above waters were compared using (a) undiluted sea water (b) 1/10 and 1/100 dilutions and plating one cc of each. Then, under standard test conditions, samples were held at room temperature (median 26° C) until arrival at the laboratory.

OBSERVATIONS AND TENTATIVE CONCLUSIONS

The preliminary observations were based on color, motility, Gram's stain, morphology, acid, gas, proteolysis, and biochemical determinative procedure. First it was noted that when using standard plate and frost slide count techniques, colony growth ran from 2 to 10 times as high on media made with local salt waters as on media made with the usual sterile fresh water (Figures 2, 3, and 4). However, the fresh water base media grew some colonies, particularly spore-bearing spreaders, that were not observed on the salt water media, and vice versa. The most varied and luxuriant colony growth was obtained with ordinary Difco nutrient agar incorporated with local marine water. The highest growth rates with most widely diverse colony formation was obtained from the turbid, shallow, brackish waters of Florida inland waterways.

Among the bacterial flora noted were large white smooth and rough *Proteus* or *Subtilis*-like spreaders, with numerous small white mucoid surface and subsurface colonies interspersed between them. The so-called chromogens

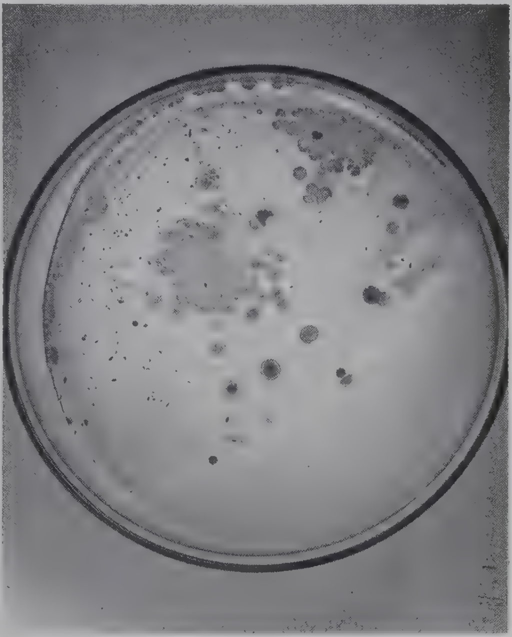


FIG. 2. Growth on medium made with fresh water. Sample from bottom Gulf water.

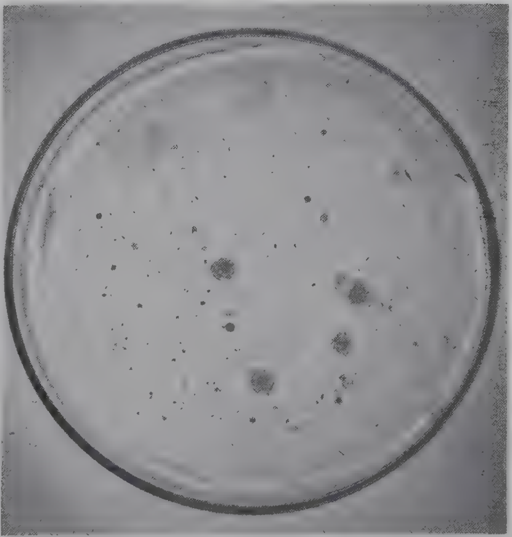


FIG. 3. Growth on medium made with salt water. Sample from surface Gulf water. Note numerous pin point colonies.

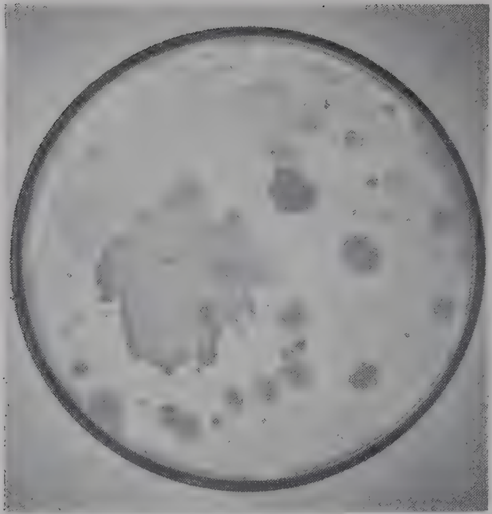


FIG. 4. Growth on medium made from sterile fresh water. Sample from surface Atlantic water. Note spreaders.

were frequently encountered and, to aid identification, pigments were classed as either carotenoids, the ether soluble pigments, or anthocyanins, the water soluble pigments. These included the pseuedomonads with blue-green water soluble pigments; Micrococcaceae, gram positive organisms with yellow or orange pigmentation colonies; and Achromobacteriaceae showing characteristic yellow to orange pigments. Some Thiorhodaceae were identified as sulfur bacteria with purple colonies to be differentiated from the *Chromobacterium violaceum* with a similar violet chromogenesis. Rhodobacteriineae (red to green photosynthetic bacteria) were frequently encountered, particularly in gulf and adjacent waters. These organisms, along with the diatoms, evidently play an important role in the balance of life between marine flora and fauna. Actinomycetes were obtained on Czapek salt water enriched media, occurring as branched rods or filamentous forms, similar to soil flora.

Additional sea bacteria identified were members of the genus *Micrococcus,* the *Sarcina aurantiacus* and *lutea,* with packets of fours, eights and bales noted. These microorganisms were present in most harbor and gulf samples and were identifiable after 48 hours incubation. Also present were some yellow and orange pigment producing *Staphylococci.* The large white rough mucoid greyish colonies found consistently in brackish waters resembled the *Bacillus subtilis* or *B. mycoides.* They appeared as aerobic, gram positive liquefiers of gelatin, spore bearing and slightly motile.

Proteus like organisms characterized as thin moist spreading colonies, rapid liquefiers of gelatin, gram negative rods with some gram negative varients were found most pravalent in bottom gulf and bay samples. They were tentatively identified as the *P. mirabilis.* Pseudomonads were isolated, as short gram negative rods which were positive in Klegler's iron slants, with typical blue green pigments which suffused into the media. They were tentatively identified as *Pseudomonas aeruginosa* (= *B. pyocaneus*).

Aerobacter aerogenes colonies were present in most samples whether in surface or bottom, clear or turbid salt waters. Confirmatory tests were run on sugars for acid and gas, on Levine's EMB, on Simmons' citrate medium which turned green to blue, and on desoxycholate medium; all were positive for *Aerobacter.*

Some gram positive mold growth, with no aerial hyphae but with rich growth on mycosal agar were identified as *Geotrichium candidum.* The red colonies which were occasionally encountered were identified as *Serratia marcensens* (= *B. prodigiosus*). Finally, according to recent literature, Endothiobacteria which contain green bacteriochlorophyll were found to be abundant in the organically rich littoral waters of the Gulf of Mexico.

Salmonella gallinarium was surprisingly identified in the Alligator Harbor waters where pelicans, gulls, terns, loons, grebes, and cormorants were frequent visitors. Reaction were as follows: Klegler's iron, —; Acid Butt and Slant, no change; Xylose, acid; Dextrose, acid; Lactose, no change; Rhamnose, —; Mannitol, acid; S.I.M. medium, —; Endo's, —; Motility, —; H_2S, —; Urea Broth, —; and Simmons' Citrate, —.

Of considerable interest in this research was the fact that many slides, particularly those immersed in brackish water, and near bottom samples, repelled all staining attempts. It must be inferred that these waters contained silicons or mineral or algal oils which repelled acidic, basic or neutral stains. Treatment of the slides with xylol, acetone, or alcohol before or after immersion was ineffective.

CONCLUSIONS

(1) Under our test sampling conditions, salt water base nutrient agar gave most varied and luxuriant bacterial and mycotic growth of colony formation of marine schizomycetes and zygomycetes or hyphomycetes.

(2) Coliforms were not found in any of our salt water samplings, but *Aerobacter* were constantly present.

(3) Micrococaceae identified as the *Sarcina aurantica* and *lutea* were frequently encountered.

(4) Silicones or oils frequently prevented the staining of slides immersed in brackish or stagnant inland salt waters, when suspended for varying periods in screened traps.

(5) The numerical incidence of bacterial flora appeared to be directly proportional to the content of suspended organic matter and zoo- and phytoplankton.

(6) Autotrophic proteolytic liquefiers of gelatin as *Proteus* or *Subtilis* like colonies were found most frequently in the bottom samples of both brackish waters and clear waters.

(7) Incubation of plates and coated slides at 37° C was conducive to very satisfactory growth rates, with plate colonies readable at 24 hours, and slide colonies at 8 hours.

(8) Bottom samples showed a higher overall numerical bacterial flora particularly in land and brackish waters than clear surface waters, especially when using salt water media.

(9) *Aerobacter* and *Proteus* groups were a fairly constant finding in all surface and bottom salt water samples.

(10) *Salmonella gallinarium* was surprisingly identified in the Alligator Harbor waters. It should be noted that aquatic bird life abounds in and around these waters.

(11) Mycotic growth was encountered in most brackish water, bottom and washed sand samples, with sporulating hyphae. Occasional aquatic fungi were noted in the clear waters of Panama City Gulf waters.

(12) The so-called chromogens, or pigment producers,

were isolated, particularly in bottom samples with reds, pinks, yellow, orange, violet, blue green and brown noted in many samples, particularly when cultured in salt water enriched nutrient agar.

(13) Some autotrophic bacteria such as the purple, green and sulfur Chlorabacteriaeceae, containing Bacteriochlorophyll were frequent invaders of the Gulf and adjacent waters. (Confirmed in "Gulf and Adjacent Waters," Fishery Bulletin No. 89, p. 217, 1954.)

(14) Crystal clear waters showed consistently less varied bacterial populations than bottom or brackish water in our samplings.

(15) *Pseudomonas pyocyaneus* was occasionally identified in marine samples.

(16) Unidentified spirilla resembling *Spironema refringens* were occasionally noted.

(17) *Aerugenosa fluorescens* with greenish yellow pigmentation were noted.

(18) *Serratia marcescens* producing the red pigment prodigiosin, was identified in the pink sand of the gulf and adjacent waters.

(19) Gram positive and negative also gram variable coci were tentatively identified as *Staphlococcus citreus* and *albus; Sarcina lutea* and *aurantica.*

(20) *Bacillus subtilis* and *mycoides* were frequent microbial invaders of all waters sampled.

(21) The Salt water media showed more numerous smooth pin-point, semi-translucent colonies than sterile fresh water media. However, large spreading rough opaque colonies were more prevalent on sterile water media.

(22) While hanging drop, dark field preparations picked from small and large colonies revealed very few actively motile rods, spore bearers were constantly encountered in our samples.

(23) These preliminary studies indicate such a wide variety of marine bacterial and mycotic flora encountered in the gulf and adjacent waters, as a result of using local salt water media, that further marine microbiological research based on bacterial physiology and chemistry should be forthcoming.

Charles A. Bryan
and
Arthur H. Bryan

Jacksonville University
Jacksonville, Florida

DENSITY OF PLAINS WOOD RAT DENS ON FOUR PLANT COMMUNITIES IN SOUTH TEXAS

Little information is available regarding the density of small rodents on rangelands. Of 125 papers reviewed by Hanson (1957), only 3 gave information on the density of wood rat dens. None of these contained data on the plains wood rat (*Neotoma micropus*).

Monson and Kessler (1940) found an average of 2.3 houses of the white-throated wood rat (*Neotoma albigula*) per acre on a 750 acre tract in Arizona and southwestern New Mexico. They reported 91.4% of the houses in use. Hanson (1957) found a mean number of 5.1 white throated wood rat houses per acre on Arizona chaparral range.

Johnson (1952) studied populations of plains wood rats in Zavala County, Texas and estimated 30 dens per acre in the mesquite-cactus communities, 10 dens per acre in the mesquite-brush communities, and essentially no dens in the mesquite savannah communities.

During the summer of 1958, plains wood rat dens were counted on 25 one-tenth acre quadrats on each of 4 plant communities on the Rob and Bessie Welder Wildlife Refuge, San Patricio County, Texas. These communities were described by Box (1957) as a mesquite-buffalo grass community, a chaparral-bristlegrass community, a bunch grass-annual forb community, and a prickly pear-short grass community.

The bunch grass-annual forb community was a true prairie dominated by seacoast bluestem (*Andropogon scoparius* var. *littoralis*) with seasonal aspect dominants of annual forbs. No wood rat dens were observed in this vegetational type.

Approximately 35% of the mesquite-buffalo grass community was covered with running mesquite (*Prosopis juliflora* var. *glandulosa*). The most common herbaceous plant was buffalo grass (*Buchloe dactyloides*). Only 3 wood rat dens were found on the 25 quadrats examined on this vegetational type; none appeared to be occupied.

The chaparral-bristlegrass community had approximately 30% of its area covered with a South Texas chaparral complex ranging from 2 to 7 feet in height. The most abundant grass in the area was plains bristlegrass (*Setaria macrostachya*). A mean number of 10.4 dens per acre was found in this plant community. The fiducial limits at the .05 level were 8.1-12.2 dens per acre. A mean number of 4.8 dens pere acre appeared to be used.

The prickly pear-short grass community had 23% of its area covered with prickly pear (*Opuntia lindheimeri*) and 22% covered with the chaparral complex. The dominant grasses were buffalo grass, curly mesquite (*Hilaria belangeri*), and windmill grasses (*Chloris* sp.). A mean number of 12.4 dens per acre was found in this community with fiducial limits of 9.0-15.8 dens per acre. A mean number of 6.4 dens per acre showed signs of being occupied.

Food particles of agarito (*Berberis trifoliata*) and granjeno (*Celtis pallida*) berries were found in dens on the chaparral-bristlegrass community. Prickly pear tunas were observed to be carried to the dens in the prickly pear-short grass community and prickly pear seed were present in wood rat feces.

The density of wood rat dens appeared to be closely associated with overhead cover. The greatest density occurred in the prickly pear communities, lesser numbers were found in the chaparral communities, dens were essentially lacking in the running mesquite communities, and houses were absent from the true prairie communities.

References

Box, Thadis W. 1957. Vegetational analyses and the determination of range condition classes on selected areas of the Welder Wildlife Refuge. Unpbl. M.S. Thesis. The Agr. and Mech. College of Texas.

Hanson, W. R. 1957. Density of wood rat houses in Arizona chaparral. Ecology **38:** 650.

Johnson, Clifford W. 1952. The ecological life history of the pack rat (*Neotoma micropus*) in the brushlands of South Texas. Unpbl. M.A. Thesis. Univ. of Texas.

Monson, Gayle and Wayne Kessler. 1940. Life history notes on the banner tailed kangoroo rat, Merriam's kangaroo rat, and the white-throated wood rat in Arizona and New Mexico. Jour. Wildlife Mgmt. **4:** 37-43.

THADIS W. BOX

DEPARTMENT OF RANGE AND FORESTRY
AGRICULTURAL AND MECHANICAL COLLEGE OF TEXAS
COLLEGE STATION, TEXAS

A METHOD OF ESTIMATING THE AGE OF PAINTED TURTLES FOR USE IN DEMOGRAPHIC STUDIES

Several workers have attempted to devise methods by which the age of turtles could be estimated. The two techniques most commonly employed have been the counting of the growth rings or annuli present on one of the laminae and the measurement of the amount of growth which occurred between successive captures. Miller (1955) and Woodbury and Hardy (1948) considered the use of the annuli of *Gopherus* unsuitable for estimating age; Cagle (1946) has shown that the counting of annuli, at least among smaller individuals, is feasible for use with *Pseudemys,* and Mattox (1935) demonstrated a positive correlation between the number of rings in the long bones of *Chrysemys* and the size of the animals. Risley (1933) plotted the length of the carapace against the number of "annual rings" in *Sternotherus.* The second technique, employing a knowledge of the growth rate of the various size classes, has been utilized for *Amyda* by Breckenridge (1955) and for *Chrysemys* by Pearse (1923) and Cagle (1954).

The procedure proposed here combines the two general methods mentioned above. A study was made of the growth annuli visible on the right abdominal lamina of 878 painted turtles, *Chrysemys picta marginata* Agassiz, captured on the Edwin S. George Reserve, Pinckney, Michigan during 1953 and 1954 and parts of 1955, 1956, and 1957. The average length of the annuli of different seasons was estimated, and the growth rate of the abdominal lamina was determined for animals of various size classes. The turtles were captured, individually marked and released immediately. At each capture the medial length of all of the annuli visible on the right abdominal lamina was measured to the nearest millimeter with a Vernier calipers. The sex of each animal with abdominal lamina of 2.0 cm or more in length was recorded; those animals with a smaller abdominal lamina were classed as juveniles.

The method of estimating age

The basic supposition in the present method of estimating age is that, ideally, the age of a painted turtle can be obtained by counting the number of growth rings or annuli on one of the laminae (Figure 1). When a turtle emerges from the nest, during March and April in the vicinity of Pinckney, the right abdominal lamina varies in length from 0.3 to 0.6 cm. The average length of this lamina was 0.54 cm in a sample of 84 hatching *Chrysemys.* There is no increase in the size of the abdominal lamina until late May or early June. From this time until late August each lamina increases in size. The limits of the lamina at emergence from the nest are indicated by a ridge, and the new growth is peripheral to this. The area within this ridge is termed the hatching annulus and is numbered annulus O. The area outside of the ridge represents the amount of growth during the first growing season, and this annulus is numbered annulus 1. The outer limits of annulus 1 will be indicated by another ridge at the inception of growth in the following growing season. In this manner a new annulus will be formed each growing season. For example, the turtle in Fig. 1 is in the fourth season of growth following emergence from the nest. It has the original annulus, annulus 0, and the 4 annuli which represent the growth of 4 seasons, annuli 1 through 4. If each turtle retained all of the growth annuli, it would be a simple matter to calculate the age of the animals.

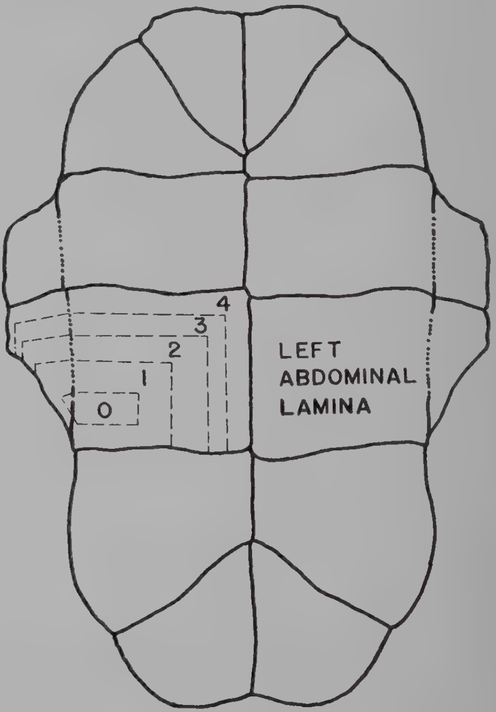


FIG. 1. Diagrammatic view of the plastron of the painted turtle showing the growth annuli or rings on the right abdominal lamina only. The turtle represented here is in the fourth season of growth following emergence from the nest in the Pinckney, Michigan region.

The use of this technique for estimating age, by counting the number of annuli, is based upon 4 assumptions. First, there is a discernible growth increment each year. This is generally true for the younger turtles up until the fifth to seventh growing seasons. Second, only one annulus is added per year. Accessory annuli, as distinguished from primary ones (those indicating the growth of an entire season) are formed during the time that shedding occurs. Approximately 28% of the juvenal turtles developed accessory annuli during the first growing season while only 2.5% did so during the third growing season. No accessory annuli were ever observed on male *Chrysemys* or on female painted turtles older than 7 growing seasons. About 3% of the females, aged 5 through 7 growing seasons, had accessory annuli. These extra rings are not permanent, and they begin to fade by fall although some persist into the next growing season. Third, no annuli are lost. This assumption is not true for all age classes since the ridges marking the limits of the annuli become obliterated with time. The older ridges begin to disappear when the animals are about 5 to 7 growing seasons old. These older ridges tend to disappear before the younger ones. Fourth, the length of the ridge along the medial border of the right abdominal lamina does not change in length after its formation. Measurements sometimes differed by 1 mm on successive captures, but this was evidently due to the gradual fading of the annuli and to error in measuring.

The overall conclusion is that a single, fairly permanent, annulus is formed each growing season but that with time the annuli fade, the older before the younger. Hence, while the age of turtles having all of the annuli present is easy to determine, it is difficult to estimate the age of those animals with annuli obliterated.

Since all of the annuli on many young turtles are present, the average length of the ridges bordering the medial side of the annuli may be computed. The average length of the ridges representing seasons one through 6 is presented in Table I for both male and female turtles. By the time the animals are older than 6, the earliest ridges, most often those of seasons one through 3, are no longer distinct so that few turtles have a complete sequence of annuli visible. Those ridges which are visible may be placed in the proper relationship if some of them can be identified. Since the variation in the length of the medial ridges for seasons one through 6 is already known, later ridges may be identified if some of them fall within the range of variation of the ridges of known age. In this manner the ridge delimiting annulus 7 in males and annuli 7 and 8 in females was identified, and the average length of these ridges was determined (Table I).

This procedure is not reliable for identifying the annuli formed in the ninth and later growing seasons, and a substitute method of estimating age must be employed. This technique is based upon the rate of growth per growing season among turtles of various size classes. The length of the medial ridge of annulus 7 averaged 2.50 cm for males of *Chrysemys*. The rate of increase in the length of this ridge averaged 0.08 cm per growing season in a sample of 34 males with abdominal lamina varying from 2.5 to 3.0 cm in length. From this rate of growth estimates may be made of the length of the annulus for seasons 8 through 13. For example, the length of the ridge delimiting annulus 8 would be 2.58 cm, and, for annulus 9, 2.66 cm. The remaining estimates are presented in Table I. The growth rate for males with an abdominal lamina greater than 3.0 cm long is so low that its use is impractical. The same procedure was followed for determining the length of annuli 9 through 13 in females (Table I). The abdominal lamina of such females increases at the rate of 0.08 cm per year.

TABLE I. The medial lengths of the annuli on the right abdominal lamina of *Chrysemys*. M = values for males; F = values for females and juveniles

Annulus of growing season	Range of annulus in cm.	Mean annulus length in cm.	Standard deviation	Number of animals measured
1 M	0.9 -1.3	1.12	0.10	39
F	0.9 -1.4	1.14	0.12	62
2 M	1.3 -1.75	1.53	0.12	39
F	1.2 -1.8	1.54	0.14	62
3 M	1.5 -2.1	1.79	0.14	39
F	1.5 -2.3	1.86	0.17	62
4 M	1.7 -2.3	2.02	0.15	33
F	1.8 -2.5	2.11	0.18	49
5 M	1.9 -2.4	2.19	0.12	35
F	2.0 -2.75	2.34	0.17	26
6 M	2.0 -2.70	2.33	0.15	22
F	2.1 -2.9	2.56	0.17	41
7 M	2.35-2.9	2.50	0.14	14
F	2.45-3.1	2.78	0.19	23
8 M	....	2.58	....	..
F	2.7 -3.4	3.01	0.21	15
9 M	....	2.66	....	..
F	....	3.09	....	..
10 M	....	2.74	....	..
F	....	3.17	....	..
11 M	....	2.82	...	..
F	....	3.25	....	..
12 M	....	2.90	....	..
F	....	3.33	....	..
13 M	....	2.98	....	..
F	....	3.41	....	..

The accuracy of the growth rates may be roughly evaluated. During the spring of 1958 Mr. Russell Mumford kindly collected some dead turtles from the periphery of Crane Pond. Of these, 4 females and 2 males could be positively identified. All had grown since they were last captured, and the approximate age of each turtle was known. Thus, the amount of growth expected between the previous and final measurements could be contrasted to the actual amount of growth as a check on the reliability of the growth rates (Table II). The observed laminar lengths correspond well with the expected values, although there is some deviation.

Use in demographic studies

The age-size data presented in Table I can now be used to estimate the age of the animals in the population sampled. If the lengths of all of the annuli visible on the abdominal lamina are recorded at each capture for each turtle, the successive annuli can be matched against

Table II. The observed and expected laminar lengths of 6 *Chrysemys* last captured several growing seasons prior to 1958 and found dead during the spring of 1958

Turtle	Age at last capture	Date of last capture	Expected lamina length in cm Mean and standard deviation	Observed lamina length in cm
Female 729...	3	Oct. 13, '54	2.39-2.56-2.73	2.6
Female 96...	4	Aug. 20, '54	2.59-2.78-2.97	2.6
Female 646...	6	Oct. 14, '54	3.09	2.7
Female 451...	8	Sept. 23, '54	3.25	3.2
Male 178.....	5	Oct. 14, '54	2.58	2.75
Male 228.....	6	July 24, '53	2.74	2.6

the values in the proper table and identified. For example, a male *Chrysemys* had 4 annuli visible on the right abdominal lamina. Their lengths were 1.8, 2.0, 2.2, and 2.3 cm. Comparing these figures with those in Table I it is easy to identify the annuli as annuli 3 through 6. Annulus 3 is 1.8 cm long, annulus 4 is 2.0 cm, annulus 5 is 2.2 cm, and the last, annulus 6 is 2.3 cm long. It is not always this easy to identify the annuli, as was the case with a female painted turtle which had 4 annuli visible. The lengths were 2.0, 2.3, 2.5, and 2.6 cm. The 4 rings were best identified as annuli 4 through 7. The fit is not exact, for it is possible that the annuli could be dated 3 through 6. In any case the age of this particular female can be estimated within a year. This is certainly better than merely stating that the turtle is over 4 years old, a subadult, or is in some other general category.

The accuracy of the method increases with the number of visible annuli. Consequently, it is very difficult to estimate the age of the larger animals. For example, a large female painted turtle with only 2 annuli visible, one 3.3 cm long, the other 3.4 cm long, could be placed only tentatively in age class 13 since the range of variation of those annuli representing seasons 9 and above is not known. Even so, the general age range of the animal can be identified. At present it appears impractical to estimate the age of those females older than 13.

It would appear that the age-size data presented in this paper would be applicable only to the Crane Pond population. The growth rate undoubtedly varies widely from place to place as a result of genetic, climatic, and biotic factors. Accordingly, separate age-size tables should be constructed for each population which is to be studied demographically. The present method of estimating the age of painted turtles can be used to envisage the population structure of a population of painted turtles within certain limits.

References

Breckenridge, W. J. 1955. Observations on the life history of the soft-shelled turtle *Trionyx ferox*, with especial reference to growth. Copeia, **1955:** 5-9.

Cagle, Fred R. 1946. The growth of the slider turtle, *Pseudemys scripta elegans*. Amer. Midl. Nat. **36:** 685-729.

———. 1954. Observations on the life cycles of painted turtles (genus *Chrysemys*). Amer. Midl. Nat. **52:** 225-235.

Mattox, Norman T. 1935. Annular rings in the long bones of turtles and their correlation with size. Trans. Ill. State Acad. Sci. **28:** 255-256.

Miller, Loye. 1955. Further observations on the desert tortoise, *Gopherus agassizi*, of California. Copeia, **1955:** 113-118.

Pearse, A. S. 1923. The growth of the painted turtle. Biol. Bull. **45:** 145-148.

Risley, Paul L. 1933. Observations on the natural history of the common musk turtle, *Sternotherus odoratus* (Latreille). Pap. Mich. Acad. Sci., Arts, and Letters **17:** 685-711.

Woodbury, Angus M. and Ross Hardy. 1948. Studies of the desert tortoise, *Gopherus agassizi*. Ecol. Monog. **18:** 145-200.

Owen J. Sexton

Department of Zoology
Washington University
St. Louis, Missouri

BLACK-TAILED JACKRABBIT CARCASSES ON THE HIGHWAYS IN NEVADA, IDAHO, AND CALIFORNIA

A 1458-mile trip taken in August 1957, in Nevado, Idaho and California, afforded us an excellent opportunity to count carcasses of black-tailed jackrabbits (*Lepus californicus*) on the highways over an extensive area in a brief period of time. This report presents the results of the count. We found that the jackrabbits are less uniformly distributed throughout Nevada than an earlier report indicates, and that they are closely associated with sagebrush in their distribution.

The carcass abundance is here assumed to reflect ambient population density. Although the carcass count has been used before as a population index (Gordon 1932, Sperry 1933, Williams and Nelson 1939, Smith 1943) its reliability has not yet been tested. Lechleitner (1958) has reviewed the difficulties of censusing jackrabbits and some of the methods that have been used. An obstacle to testing the carcass index is the lack of any other proven census technique with which to compare.

Recorded indices of jackrabbit abundance are of value in different ways: as a historical record for comparisons with later counts, and as a basis for studying relative population size in relation to habitat preference, agricultural influences, jackrabbit control, and the like.

Distribution and abundance

The distribution and abundance of the carcasses are shown in Figure 1. Counts were made separately for each one-mile sector of road and grouped by 2-mile intervals. Highways are shown diagrammatically as straight bands between selected towns.

Hall (1946, p. 602) found this hare about equally abundant throughout the parts of Nevada we traveled. In contrast, we found that the carcasses were most abundant in the northern and eastern parts, least abundant from Reno to Lovelock and south to Las Vegas and Caliente. It appears from our data that the southwestern

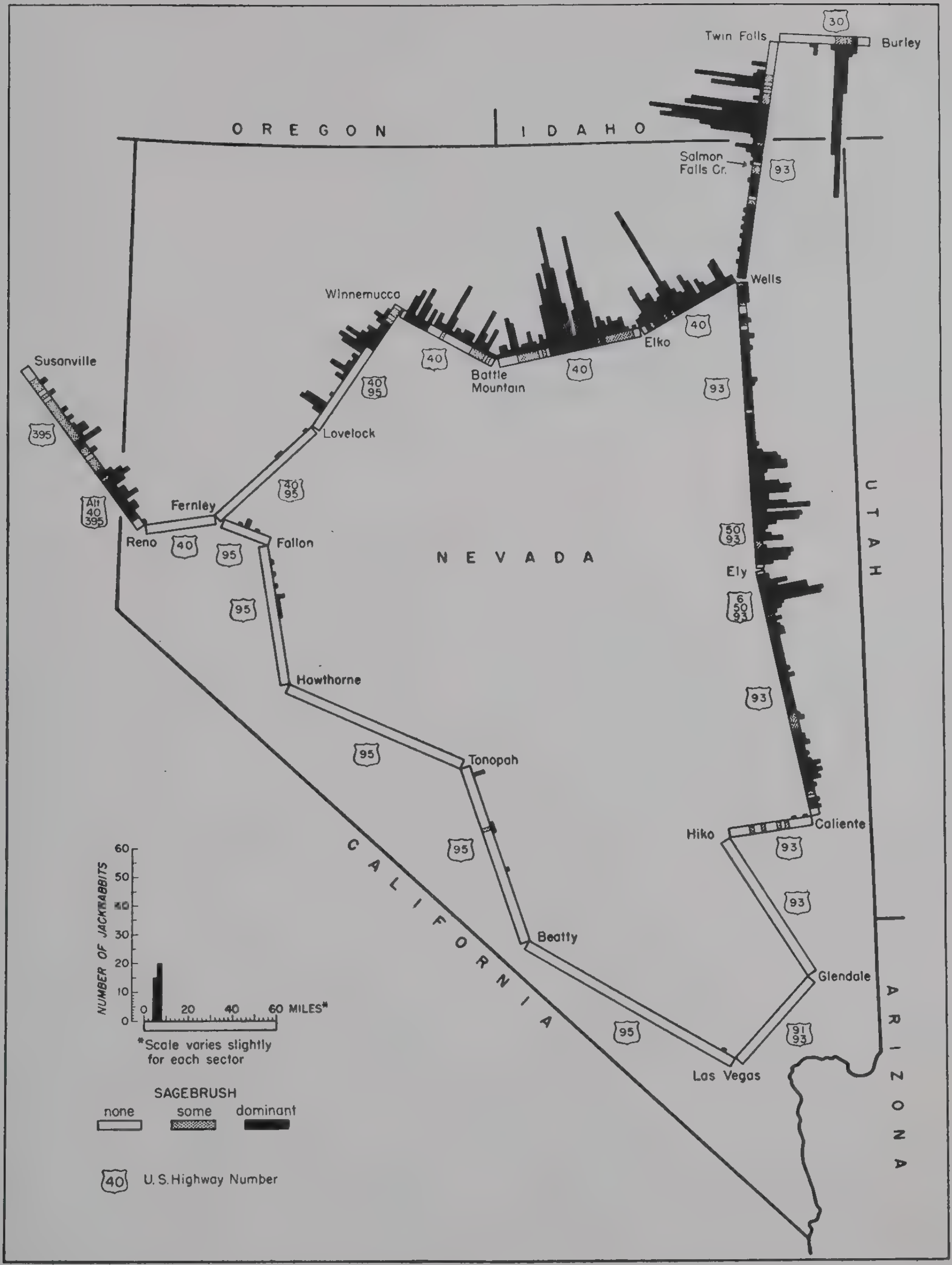

30
Twin Falls
Burley
O R E G O N
I D A H O
Salmon Falls Cr.
93
Wells
Winnemucca
Susanville
395
Alt 40 395
40 95
Lovelock
40
Battle Mountain
Elko
Fernley
Reno
Fallon
N E V A D A
U T A H
50 93
Ely
6 50 93
Hawthorne
Tonopah
Hiko
Caliente
C A L I F O R N I A
Beatty
Glendale
A R I Z O N A
91 93
Las Vegas
NUMBER OF JACKRABBITS
60
50
40
30
20
10
0
0 20 40 60 MILES*
*Scale varies slightly for each sector
SAGEBRUSH
none
some
dominant
40 U. S. Highway Number

Fig. 1. The incidence of jackrabbit carcasses on highways is shown by the heights of the bars. The relative abundance of sagebrush is shown by shading on the highways bands.

populations were at lower levels than those in northern and eastern Nevada and in northeastern California at the time of our count.

Carcasses tended to occur in groups, as often happens with plants and animals in nature. The greatest number of carcasses in any 2-mile sector was 54 near Burley, Idaho (Fig. 1).

We were interested in the effects of vegetation on jackrabbit distribution, so for each of the one-mile sections we recorded the presence or absence of some of the outstanding shrubs. Inspection of the data showed that sagebrush (*Artemisia,* spp.) was the plant with distribution conforming most nearly with the distribution of carcasses. This relationship is shown in Fig. 1 where most of the localities with carcasses also have sagebrush. The relationship is not perfect. Jackrabbit carcasses north of Lovelock were associated with sheep-fat (*Atriplex confertifolia*) rather than with sagebrush. Dense sagebrush stands south of Wells had few carcasses. The nature of our data does not permit precise mathematical evaluation of the degree of association between jackrabbits and sagebrush (Greig-Smith 1957).

References

Gordon, K. 1932. Rabbits killed on an Idaho highway. Jour. Mammalogy **13:** 169.

Greig-Smith, P. 1957. Quantitative plant ecology. New York, Academic Press.

Hall, E. R. 1946. Mammals of Nevada. Berkeley, Univ. Calif. Press.

Lechleitner, R. R. 1958. Movements, density and mortality in a black-tailed jackrabbit population. Jour. Wildlife Mgt. **22:** 371-384.

Smith, C. F. 1943. Rabbit mortality on an Idaho highway. Jour. Mammalogy **24:** 262-264.

Sperry, C. C. 1933. Highway mortality of rabbits in Idaho. Jour. Mammalogy **14:** 260.

Williams, C. S. and M. C. Nelson. 1939. Highway mortality of rabbits in Idaho. Jour. Mammalogy **20:** 380-382.

HAZEL B. ADAMS[1]
AND
LOWELL ADAMS

CALIFORNIA FOREST AND RANGE EXPERIMENT STATION[2]
BERKELEY, CALIFORNIA

---

[1] Susanville, California.

[2] Maintained by the U.S. Forest Service, Department of Agriculture in cooperation with the University of California.

OCCURRENCE OF EXTREMELY SMALL OVIGEROUS CRABS (*CALLINECTES* SP.) IN COASTAL NORTH CAROLINA

The smallest adult female blue crab (*Callinectes sapidus* Rathbun) reported in the literature was 80 mm wide and 35 mm long (Hay and Shore 1918). On August 6, 1958 two smaller adult female crabs (*Callinectes* sp.), in an ovigerous condition, were caught by a shrimp trawl approximately one mile south of the entrance to Silver Lake, Ocracoke Island, North Carolina (Table I). They were taken over a sand, mud, and seaweed bottom in water ranging from 4 to 15 feet in depth. Surface water temperature was 26.8° C and surface salinity 21 $^0/_{00}$.

TABLE I. Measurements of small ovigerous crabs, *Callinectes sapidus?* taken in 1958

Measurement	Crabs caught off Ocracoke Island		Crab caught off Radio Island
	A	B	C
Length of carapace mm	23.3	24.1	22.2
Width of carapace mm	55.0	55.0	52.3
Fronto-orbital width mm	19.4	20.8	19.1

The frontal outline and other external characteristics of these adult crabs, except for their small size, resemble *Callinectes sapidus* Rathbun. W. A. Van Engel of the Virginia Fisheries Laboratory, and F. A. Chace, Jr. of the United States National Museum examined these crabs, and both agree that they appear to be *C. sapidus* Rathbun. D. G. Cargo, Maryland Department of Research and Education, also examined the crabs and stated that ". . . of the presently described species (Rathbun 1930), these most closely correspond to the published descriptions of *Callinectes sapidus.*" Mr. Cargo, who is familiar with measurements taken on 14,000 adult female blue crabs—the smallest of which was 36 mm in length, further stated ". . . it is difficult to reconcile that an adult of this species could develop at a length of 24 mm."

Another extremely small ovigerous crab was collected on October 23, 1958 by C. M. and T. G. Roberts of the U. S. Radiobiological Laboratory, Beaufort, North Carolina (Table I). This crab, caught in a haul seine on the eastward shore of Radio Island, Morehead City, North Carolina, also resembled *C. sapidus* and was identical in frontal outline and other characteristics with the 2 caught off Ocracoke Island.

The measurements of the 3 crabs reported herein were made in a manner prescribed by Rathbun (1930). Rathbun (1896), in describing the blue crab, stated that adult females normally vary from 5 to 7 inches (127 to 178 millimeters) in width.

If the 3 specimens of ovigerous crabs described above are *C. sapidus* Rathbun, which is the critical opinion of Messrs. Van Engle, Chace, and Cargo, then they are the smallest adult females of this species so reported. It is not known whether these dwarf forms of *C. sapidus* normally occur in the areas in which they were collected, or whether they are the result of genetical or environmental factors influencing growth and thereby causing dwarfism.

References

Hay, W. P. and C. A. Shore. 1918. The Decapod Crustaceans of Beaufort, N. C., and the surrounding region. Bull. U. S. Bur. Fish. (1915-16), **35:** 369-476.

Rathbun, M. J. 1896. The genus Callinectes. Proc. U. S. Nat. Mus. (1895) **18:** 349-375.

———. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. U. S. Nat. Mus. Bull. 152.

K. J. FISCHLER

BUREAU OF COMMERCIAL FISHERIES
BIOLOGICAL LABORATORY
BEAUFORT, NORTH CAROLINA

THE FOOD OF THE STARFISH, *PISASTER OCHRACEUS*, ALONG THE CALIFORNIA COAST

Although the starfish *Pisaster ochraceus* (Brandt 1835) is one of the most conspicuous animals to be found along the rocky shores of the Pacific Coast from southern Alaska to Baja California, its natural history is poorly known. That the diet is varied is indicated by several workers, though observations have been for the most part incidental rather than systematic. Stohler (1930) reports *Pisaster* using *Mytilus californianus, Acanthina spirata, Ischnochiton cooperi,* and *Mopalia muscosa* as food at Moss Beach, San Mateo County, California. It has been mentioned by Allen (1939) that ". . . large starfish are always present on the columns (of the Scripps Institution of Oceanography pier pilings), and nearly always it is possible to see within a foot or two on all sides of one a striking array of empty shells of mussels which have been devoured." Hewatt (1937) notes *Pisaster ochraceus* feeding on *Mytilus californianus* at Mussel Point in Monterey Bay. Ricketts and Calvin (1939, 1952) state that *P. ochraceus* feeds on mussels, barnacles, and snails throughout its range. Starfish in Southern California have been found feeding on mussels (*Mytilus californianus* and *M. edulis*), barnacles, snails, small abalones, and small crabs (MacGinitie and MacGinitie 1949). The possibility of starfish using abalone for food is also suggested by Livingstone (1952), and he states that "Areas in which the diver reported an unusual abundance of starfish yielded few abalone." D. Mills (unpublished notes 1952) examined feeding starfish at Moss Beach, and his results indicate that the animals used as food there were essentially the same as those used in Monterey Bay and elsewhere. Fisher and Leitch (1954) state that *P. ochraceus* have a ". . . predilection for mussels, barnacles, and limpets." The planting of oysters in British Columbia waters has presented a new source of food to the starfish, and it now feeds on *Crassostrea gigas* in these waters (Elsey 1933, Quayle 1954).

The present study presents an attempt to answer two questions: (a) What organisms are utilized by *Pisaster ochraceus* for food? and (b) Is there a relationship between availability of a food organism in the environment and the relative frequency with which it is eaten?

Frequency with Which Various Food Species are Taken by *P. ochraceus*

Periodic daytime examinations of starfish were made at low tide in various regions of the Monterey Bay area by prying starfish free of the substrate, turning them over, and examining the oral area. If an animal was feeding, the food was generally well tucked into this region (Figure 1). If the prey was rather small, it would often be completely covered by the soft folds of the everted starfish stomach but could be readily determined without injury to the starfish by gently teasing the organism out of the oral region with a pair of forceps.

Data on the frequency with which various food species are taken by *P. ochraceus* in the Monterey Bay area are listed in Table I. The figures shown are based on examination of approximately 3,450 starfish on 70 separate field surveys. The mean number of individuals examined on each survey was about 50 and an average of about 18.0% of the starfish were feeding at the time they were examined. Young of *Pisaster ochraceus* usually feed on young specimens of the same food species taken by older starfish, but they do use two animals that the larger starfish seldom take because of their small size: the nestling clam, *Hiatella arctica,* and the small polychaete tubeworm, *Spirorbis* sp.

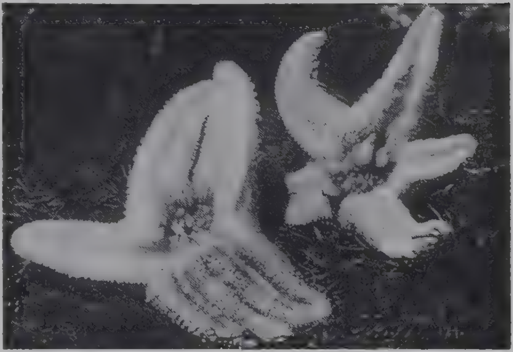


Fig. 1. View of the hollow oral region of starfishes feeding on *Tetraclita squamosa rubescens* and *Mitella polymerus.*

Personal examination of starfishes feeding along the California coast at La Jolla, Newport Beach, Palos Verdes, and San Simeon, and reports from Moss Beach, San Mateo County (Stohler 1930, Mills, unpublished notes 1952) have indicated that the starfish feeds on much the same food organisms throughout this portion of its range. A few food differences were noted in different areas. *P. ochraceus* has been observed using the rock oyster, *Chama pellucida,* for food in Newport Bay. This species is uncommon in Monterey Bay. Stohler (1930) collecting at Moss Beach found a starfish feeding on an *Ischnochiton cooperi.* Mills, in the same region, collected 2 starfish feeding on *Balanus cariosus* and *Pagurus* sp. respectively.

In the laboratory aquaria *Pisaster* has been observed feeding on a variety of organisms as shown in the following list:

Eudistylia polymorpha (polychaete)
Urechis caupo (echiuroid)
Mitella polymerus (barnacle)
Balanus glandula (barnacle)
Balanus nubilis (barnacle)
Blepharipoda occidentalis (sand crab)
Haliotis cracherodii (abalone)
Haliotis rufescens (abalone)
Acmaea testudinalis scutum (limpet)
Acmaea digitalis (limpet)
Calliostoma costatum (snail)
Tegula funebralis (snail)
Thais emarginata (snail)
Mytilus californianus (mussel)
Mytilus edulis (mussel)
Crassostrea gigas (oyster)
Ostrea lurida (oyster)
Clinocardium nuttallii (clam)
Schizothaerus nuttallii (clam)
Tivela stultorum (clam)
Loligo opalescens (squid)
Strongylocentrotus purpuratus (sea urchin)
Pisaster ochraceus
Ascidia ceratodes (tunicate)

The animals fed upon included species which do not ordinarily occur in the environment with *Pisaster* in the field. Examples of the latter type of laboratory prey are *Urechis caupo, Blepharipoda occidentalis, Ostrea lurida, Schizothaerus nuttallii, Clinocardium nuttallii, Tivela stultorum,* and *Loligo opalescens.* Included in the list of animals above are species that occasionally or frequently do occur in the same habitat as the starfish but which have never been observed to be used by *Pisaster* for food in the field. The tube-dwelling polychaete worm, *Eudistylia polymorpha,* and the simple ascidian, *Ascidia ceratodes,* fall in this category. Three other species, *Haliotis cracherodii, Haliotis rufescens,* and *Strongylocentrotus purpuratus* are often found in the same habitat as *P. ochraceus.* They were frequently available to *P. ochraceus* as food in laboratory tanks, but they were seldom taken unless they were weakened or dead.

A specimen of the ochre starfish was collected on the mudflats of Elkhorn Slough near Moss Landing, Monterey County, a most unusual situation in which to find *P. ochraceus.* The animal was feeding on a mass of the phoronid worm, *Phoronopsis viridis.*

The Frequency with Which Various Organisms Are Eaten in Relation to Their Abundance in the Environment

It has been generally considered that *P. ochraceus* uses the California mussel, *Mytilus californianus,* as its chief food source. Ricketts and Calvin (1939, 1952) state, "We have found *Pisaster* feeding on mussels, predominantly, less frequently on barnacles and snails, and rarely on goose barnacles and limpets." Certainly it is true that the mussel is used as the predominant food source in mussel beds, but this cannot be said of the large numbers of *P. ochraceus* that live in other habitats. While there is a preference for certain types of food, the extent to which particular species are taken varies with the local situation within any given geographical area.

Four separate rocky intertidal areas, all inhabited by *P. ochraceus* but representing 4 somewhat different ecological situations in the Monterey Bay region, were chosen for examination. A comparison of the conditions in the investigated areas is summarized in Table II. Areas 1-3 form a graded series in terms of exposure to wave shock and in the types of food available to *P. ochraceus.* Area 4 was not chosen to compare physically with the other regions, but was picked because the type of food available here differed markedly from that in the other three study areas.

Figure 2 compares field observations on feeding *Pisaster* in the 4 areas, in relation to the relative abundance of each of the food species in the environment. The data on Area 1 (primarily a mussel bed) show that mussels and acorn barnacles are eaten roughly in proportion to their abundance in this region, and form the bulk of the diet of the starfish here. Interestingly enough, *Mitella polymerus,* while second only to *Mytilus* in abundance, ranks fourth in importance as a food species for *Pisaster.* In Area 2 the two acorn barnacles predominate in the diet and serve as food sources in order of their abundance. Other animals common to this region are eaten only sporadically. In Area 3 the two acorn barnacles are again the most abundant and available species and the major food of *Pisaster,* but the order of their abundance and of their importance to the starfish are the reverse of Area 2. The chiton, *Mopalia muscosa,* is taken by the starfish more often than its abundance would suggest. *Mytilus californianus* was used as food on 2 separate occasions, though there are no mussels growing in this area. It is probable that the specimens eaten were washed in from a rocky island located several hundred feet to the north of this region. Area 4 provides a most interesting contrast to the others. The 3 organisms which dominate the diet of *Pisaster* in Areas 1-3 (*Mytilus, Balanus,* and *Tetraclita*) are scarce or absent here. Instead, the most abundant organisms are sea urchins and black abalones, which are very rarely used by the starfish for food. In Area 4 *Pisaster* feeds primarily on gastropods and on the chiton, *Mopalia muscosa.*

Table I. Food eaten in the field by 633 *Pisaster ochraceus* in the Monterey Bay area, January 1953 to January 1955. Starfish of all ages are included. Number and per cent of feeding starfish are shown for each food species

Species (Group)	Number of Cases Observed	% of Feeding Starfish
Balanus glandula (barnacle)	191	30.1
Tetraclita squamosa rubescens (barnacle)	162	25.6
Mytilus californianus (mussel)	108	17.0
Tegula funebralis (snail)	35	5.5
Acmaea scabra (limpet)	25	3.9
Mitella polymerus (barnacle)	25	3.9
Mopalia muscosa (chiton)	21	3.3
Haliotis cracherodii (abalone)	9	1.4
Thais emarginata (snail)	8	1.3
Balanus nubilis (barnacle)	8	1.3
Spirorbis sp. (polychaete)	5	0.7
Hiatella arctica (clam)	4	0.6
Balanus tintinnabulum (barnacle)	3	0.5
Tonicella lineata (chiton)	3	0.5
Littorina scutulata (snail)	2	0.3
Crepidula nummaria (limpet)	2	0.3
Tegula brunnea (snail)	2	0.3
Pachygrapsus crassipes (crab)	2	0.3
Dodecaceria fistulicola (polychaete)	2	0.3
Cirolana harfordi (isopod)	2	0.3
Mytilus edulis (mussel)	2	0.3
Katherina tunicata (chiton)	1	0.2
Mopalia hindsi (chiton)	1	0.2
Nuttallina californica (chiton)	1	0.2
Acmaea digitalis (limpet)	1	0.2
Acmaea testudinalis scutum (limpet)	1	0.2
Acmaea pelta (limpet)	1	0.2
Acanthina spirata (snail)	1	0.2
Loligo opalescens (squid)	1	0.2
Strongylocentrotus purpuratus (sea urchin)	1	0.2
Cancer antennarius (crab)	1	0.2
Sponge-unidentified	1	0.2
Phoronopsis viridis (phoronid)	1	0.2

Discussion

It is apparent that while *P. ochraceus* will feed on a wide variety of animals, it attacks primarily the molluscs and barnacles most abundant in its vicinity. Even then it exhibits a clear "preference" for the sessile mussels and acorn barnacles.

Gastropods are not eaten in proportion to their abundance; they tend to be eaten less often than their numbers would suggest where mussels or acorn barnacles are available (Areas 1 and 3), and more often where these forms are rare or absent (Area 4). This may be explained partly in terms of starfish food "preference" and

TABLE II. A comparison of the four major habits studied

Area	1	2	3	4
Location	Mussel Point, Pacific Grove, California	Mussel Point, Pacific Grove, California	Mussel Point, Pacific Grove, California	Point Lobos Reserve State Park, Monterey County, Calif.
Substrate	Granite	Granite	Granite	Sedimentary conglomerate
General topography	60 yards off-shore at high tide, granitic outcroppings surrounded by deep channels, many crevices, few boulders	50 yards off-shore, large outcroppings, numerous boulders and shallow crevices, many tide pools, sheltered by granite ridge	Characterized by mass of projecting bedrock which forms part of shoreline at high tide, many boulders and crevices, few tidepools	Cove protected by sea wall, channel through wall allows strong surge, elongated crevices, small boulders
Protection from direct wave impact	Slight	Almost complete	Complete except during storms	Almost complete for most of the area
Protection from strong surge	Very slight	Slight	Excellent	Very slight
Abundance and ease of location of *P. ochraceus*	Common, readily located	Very common, easily located but many well hidden	Common, most starfish hidden and difficult to find	Uncommon, most well hidden and difficult to find
Most characteristic animals present	*Mytilus californianus,* *Mitella polymerus* *Anthopleura xanthogrammica* *Nuttallina californica* *Lottia gigantea*	*Tetraclita squamosa rubescens* *Balanus glandula* *Haliotis cracherodii*	*Tetraclita squamosa rubescens* *Balanus glandula* *Acmaea scabra* *Tegula funebralis* *Anthopleura elegantissima*	*Strongylocentrotus purpuratus* *Haliotis cracherodii* *Acmaea scabra*
Most characteristic plants present	*Laminaria andersoni* *Macrocystis* sp. *Iridaea lineare* *Microcladia coulteri* *Egregia menziesii*	*Pelvetia fastigiata* *Iridaea lineare*	*Fucus furcatus* *Porphyra perforata* *Egregia menziesii* *Ulva lactuca*	*Iridaea* sp. *Egregia menziesii* *Ulva lactuca* *Costaria costata*

partly in terms of escape responses shown by certain gastropods (*Tegula* spp., *Acmaea* spp., and *Haliotis* spp.) to contact with, or to the near presence of, *P. ochraceus* (Haderlie unpublished 1947, MacGinitie and MacGinitie 1949, Bullock 1953, Feder 1956). The behavior of the abalone and other gastropods in the presence of *P. ochraceus* will be treated in detail in a paper now in preparation.

The sea urchin, *Strongylocentrotus purpuratus,* is very abundant in Area 4, yet it is seldom used as food. In laboratory tanks a starfish will only feed on weakened or dead urchins, indicating that a healthy *S. purpuratus* cannot be successfully attacked by *Pisaster.* Sea urchins have been shown effectively to resist starfish attack by specialized responses (Prouhou 1890, Flattely and Walton 1922).

SUMMARY

Food studies of *Pisaster ochraceus* (Brandt) in the region of Pacific Grove, California show that the starfish uses at least 29 different species for food in the field, and will use at least 16 others under aquarium conditions. It is, therefore, a real or potential predator on many intertidal animals. Arthropods and molluscs are best represented in the diet. The starfish shows a decided tendency to select certain species when available, especially the mussel *Mytilus californianus* and the acorn barnacles, *Balanus glandula* and *Tetraclita squamosa rubescens.*

The diet of *P. ochraceus* varies with the local ecological situation; certain sedentary or slow-moving animals are fed upon more or less in proportion to their abundance and availability while others are not. The mussel, *Mytilus californianus,* is used by the starfish as the main source of food in the regions of *Mytilus-Mitella* beds, and the two barnacles, *Balanus glandula* and *Tetraclita squamosa rubescens,* are the main food sources in regions not suitable for *Mytilus* growth. *Mytilus* and/or barnacles form approximately 80% of *Pisaster's* diet in these areas. In areas where neither the barnacles nor the mussels are abundant *Pisaster* turns more to gastropods and chitons and tends to be less dependent on any one particular species.

Some abundant and apparently available species are rarely eaten. These are species such as *Haliotis cracherodii* and *Strongylocentrotus purpuratus;* which appear to have developed means of escape from, or of defense against, the starfish.

REFERENCES

Allen, W. E. 1939. Cutthroat competition in the sea. Sci. Mo. **49**: 111-119.

Bullock, T. H. 1953. Predator recognition and escape responses of some intertidal gastropods in the presence of starfish. Behavior **2**: 130-140.

Elsey, C. R. 1933. Oysters in British Columbia. Biol. Bd. Can., Bull. **34**: 1-34.

Feder, H. M. 1956. Natural History Studies on the Starfish *Pisaster ochraceus* (Brandt 1835) in the

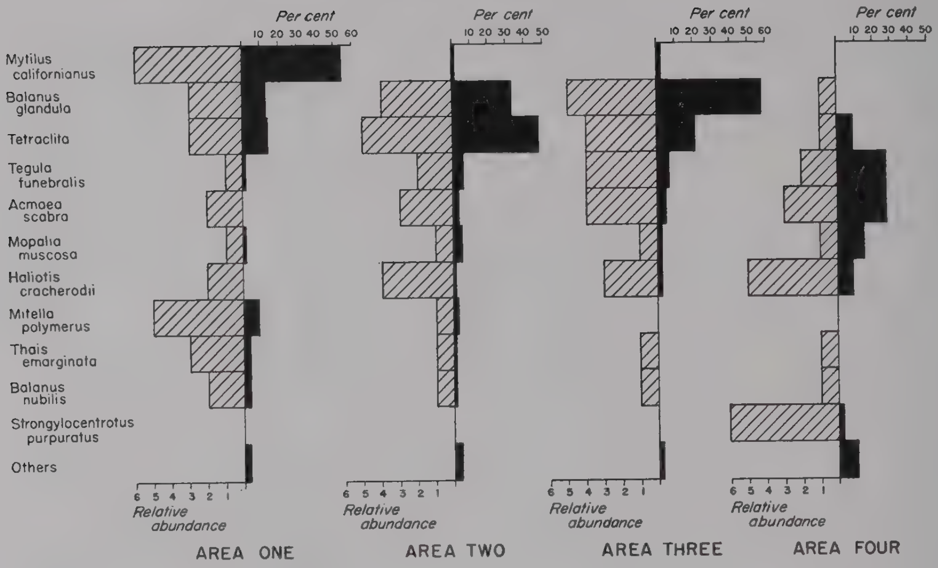


FIG. 2. A comparison of *Pisaster* diet in the four study areas. For each food species "relative abundance" in the environment and relative frequency with which it is eaten are shown. The cross-hatched bars represent the "relative abundance" of particular food species within each study area (Qualitative estimates are based on a scale of 0-none to 6-very abundant). The solid bars represent the % of feeding starfish eating a particular food species within each study area.

Monterey Bay Area. Unpublished doctoral dissertation, Stanford University.

Fisher, W. K. and J. L. Leitch. 1954. Life between the tides (in State of California Div. of Beaches and Parks, Dept. of Nat. Res., Pt. Lobos Res. State Park, Calif. Interpretation of a primitive landscape: 71-77).

Flattely, F. W. and C. L. Walton. 1922. The biology of the sea-shore. New York: Macmillan.

Hewatt, W. G. 1937. Ecological studies on selected marine intertidal communities of Monterey Bay, California. Amer. Midland Nat. **18:** 161-206.

Livingstone, R. 1952. Preliminary investigation of the southeastern Alaska abalone. Part I. Exploratory diving. Comm. Fish. Rev. **14:** 8-16.

MacGinitie, G. E. and N. MacGinitie. 1949. Natural history of marine animals. New York: McGraw-Hill.

Prouhou, H. 1890. Du rôle des pédicellaires gemmiformes des oursins. C. R. Acad. Sci. **111:** 62-64.

Quayle, D. B. 1954. Growth of the purple seastar. Oyster Bull., Shellfish Laboratory, Ladysmith, B. C. **5:** 11-13.

Ricketts, E. and J. Calvin. 1939. Between Pacific Tides. Stanford University Press.

———. 1952. Between Pacific Tides. 3d ed., rev. by J. W. Hedgpeth, Stanford University Press.

Stohler, R. 1930. Gewichtsverhaltnisse bei gewissen marinen Evertebraten. Zool. Anz. **91:** 149-155.

HOWARD M. FEDER[1]

STANFORD UNIVERSITY
HOPKINS MARINE STATION

---

[1] Present address: Hartnell College, Salinas, California. I wish to thank Dr. D. P. Abbott for advice and constructive criticism during the course of this work.

CORIXID INSECTS AS PART OF THE OFFSHORE FAUNA OF THE SEA

Various shore, bay and brine pool insects have been noted by various workers (*cf.* Pearse 1950). Darwin (1839, p. 24) listed members of the Hydrophilidae from salt water lagoons in Brazil and the senior author found *Hydrophilus triangularis* in Aransas Bay, Texas (Gunter 1952). Chilton (1905) found a water beetle swimming among the sea weed in a tide pool in New Zealand. Darwin (1839, p. 186) also gave an account of 8 genera of insects found swimming in the sea 17 miles off Cape Corrientes. Four were aquatic and 4 were not, including one scarab, and he evidently considered the case accidental. These occurrences are marginal, and some are accidental, and it is generally accepted that water striders (*Halobates*) are the only insect fauna of the high seas.

Therefore, the presence of corixids as a part of the fauna of offshore waters is of considerable theoretical interest. The first instance was noted 11 miles off Grand Isle, Louisiana in a plankton tow made just beneath the surface on December 3, 1958. We then searched through 29 more preserved tows made by the junior author off the Mississippi coast. Three more corixids were found. With the use of the recent summary of aquatic Hemiptera of the State of Mississippi (Wilson 1958) all specimens were identified by D. R. Moore, verified by E. A. Richmond, as *Trichocorixa verticalis* (Fieber). The data are given in Table I.

TABLE I. Records of *Trichocorixa verticalis* from offshore plankton tows in the Gulf of Mexico (Louisiana and Mississippi)

Date	Locality	Water T °C	Salinity ‰	Sex
3/25/58	G.C.R.L. Sta. #8, 15 mi. SE by E of Dog Keys Pass, Mississippi	16.7	32.0	♀
4/22/58	G.C.R.L. Sta. #9, 20 mi. SE by E of Dog Keys Pass	22.0	26.3	♂
5/30/58	G.C.R.L. Sta. #7, 10 mi. SE by E of Dog Keys Pass	27.5	26.1	♀
12/ 3/58	Grand Isle Sta. 5 #3, 11 mi. S of Grand Isle, Louisiana	19.5	32.3	♂

According to Percy Viosca, Jr. (personal communication), corixids are sometimes extremely abundant in tide pools on the Chandeleur Islands. Wilson (1958) listed *T. verticalis* at several locations near Bay St. Louis, Mississippi and specifically noted its predilection for salt and briny waters. Therefore, it is not suprising that this species lives in adjacent bay waters of low salinity. However, it is surprising to find it so far offshore in waters of fairly low turbidity, high salinity and greenish blue color, which, in terms of the mariner, are the high seas. It should be noted that this account does not set offshore limits.

We have little data on abundance. Tows were 20 minutes long and were made with half meter nets. Four specimens were taken in 49 hauls. In these waters the insects seem not to be common nor extremely rare.

REFERENCES

Chilton, C. 1905. Note on a water-beetle found in sea-water. Trans. and Proc. New Zealand Institute. **38:** 63.

Darwin, C. 1839. Journal of Researches into the Geology and Natural History of the various countries visited by H.M.S. Beagle. Facsimile Reprint, 1st Ed.) New York. Hafner Publishing Co.

Gunter, G. 1952. *Hydrophilus* in salt water. J. New York Entom. Soc. **60:** 90.

Pearse, A. S. 1950. The Emigrations of Animals from the Sea. Dryden, N. Y. The Sherwood Press.

Wilson, C. A. 1958. Aquatic and semiaquatic Hemiptera of Mississippi. Tulane Studies Zool. **6:** 115-170.

GORDON GUNTER
J. Y. CHRISTMAS
GULF COAST RESEARCH LABORATORY
OCEAN SPRINGS, MISSISSIPPI

NOTES ON THE ECOLOGICAL CONCEPTS OF HABITAT, BIOTOPE AND NICHE

During the past few years interest has been high among ecologists in defining more precisely terms used to describe certain basic ecological concepts (see Friederichs 1958, Hutchinson 1957, Ross 1957 and 1958, Savage 1958 and Udvardy 1957 in the discussion). None are more basic, yet more inadequately defined, than the terms habitat and ecological niche. Although I do not have all the ecological literature available to me, which will account for the incompleteness of my references, the more important ones leading to my ideas of the proper usage of these terms are cited in support of the definitions here proposed.

Habitat is such a generally accepted, understood and used term that few ecology textbooks above the elementary level bother with its proper definition. Certainly the biology student thinks about the habitat as referring to a species, or other, smaller natural population unit; it is an abstraction of the essential physical factors and of the essential co-inhabitant biota, in a locality where individuals of that population regularly live and reproduce. Clements and Shelford (1939) recommended that the concept be restricted to the place of habitation with its physical elements only, but general usage remained unchanged despite their plea.

Often synthetic characteristics are used in descriptions of habitats for quicker understanding, instead of the essential ones that an analysis of the animal's requirements eventually would reveal in an ecological study. For example, in the case of the Tree Pipit (*Anthus trivialis*) a high perch for territorial singing is an essential minimum factor of the habitat (Lack 1933). Another is the openness of the ground where this bird feeds (Lack *l.c.*, Svärdson 1949), yet its habitat is synthetically described for Scandinavia as "pine heathers, logged areas and forest openings" (Original in Swedish, Peterson *et al.* 1955).

Often two terms are used as being synonymous with habitat: the *biotope* and the *niche*. Founders of the biotic community concept discovered that individual units of well defined communities occur almost always among similar environmental circumstances (*e.g.* Hesse 1924, Friederichs 1927). Thus biotic communities have their habitats (Odum 1953) and Gams (*fide* Tischler 1949) introduced the term biotope for this concept.

Although ecologists and ecologically conscious zoologists retained and are using biotope in continental Europe in this sense, we find that in the German, Swedish, Hungarian and other literature on faunistic and life history subjects it very often replaces the correct and equivalent term for habitat (*Standort* in German, *hemvist* in Swedish). Some, perhaps more cautious authors use biotope seemingly in the original usage and refer to species occurring in or occupying a certain biotope, although they really mean its habitat. Certainly the most widespread misuse of the term is found in such statesments as ". . . the biotope of a species." Two good examples of these type of references are (1) "*Ammomanes grayi* bewohnt offenbar zwei sehr unterschiedliche Biotope" (Hoesch

1958: 428); and (2) "*Phormoplectes insignis.* Biotope: Urwaldreste und tropische Galeriewald" (Heinrich 1958: 412).

With increased interest in synecology it would be desirable to reserve the term biotope for *the habitat of biotic communities* and only use it with reference to a single species when its community relationships are discussed. In other words, the species has a habitat but it does not have a biotope. The biotope harbours instead, a biotic community.

Confusion of the habitat concept is also apparent in references to the ecological niche. Grinnell, probably the first naturalist to employ this term, has often been quoted as meaning by niche a subdivision of the habitat (Dice 1952), or using the term in the sense of place (Clements and Shelford 1939, cf. also Carpenter 1938).

I will try to show that Grinnell's concept of niche, like that of Elton, refers to essential elements of the environment utilized by the animal, and so the two concepts are compatible. Grinnell's is the earlier and broader concept for his also includes elements of the physical environment. The quotations that follow show how Grinnell's concept developed throughout his years of observation and thinking.

"Every animal tends to increase at a geometric ratio, and is checked only by limit of food supply It is only by adaptations to different sorts of food, or modes of food getting, that more than one species can occupy the same locality. Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other"; (Grinnell 1904: 375-376).

". . . these various circumstances, which emphasize dependence upon cover, and adaptation in physical structure and temperament thereto, go to demonstrate the nature of the ultimate associational niche occupied by the California thrasher. This is one of the minor niches which with their occupants all together make the chaparral association. It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships" (Grinnell 1917: 433).

". . . Diversity of environments, otherwise habitats has been essential to the evolution of . . . vertebrate animals. Evolution of environments came first—comes first; it is going on continually. . . ."

". . . I would call attention to the great number of *similar* ecologic types of animals which are developed in widely separate regions and which are derived from *unrelated stocks*" (discusses the Californian kangaroo rat and the jerboa of the Sahara, and the unrelated tree-creepers of North and South America).

"Habitats have been variously classified by students of geographical distribution. Some of us have concluded that we can usefully recognize, as measures of distributional behavior, the realm, the region, the life-zone, the fauna, the subfauna, the association, and the ecologic or environmental niche. The latter, ultimate unit, is occupied by just one species or subspecies; if a new ecologic niche arises, or if a niche is vacated, nature hastens to supply an occupant . . .." (Grinnell 1924: 226-227).

"In studying these matters, I have come to use the term 'ecologic niche.' This expression is intended to stand for the concept of the ultimate distributional unit, within which each species is held by its structural and instinctive limitations. . . ." He then examines what he calls the 'two critical factors' the food, and consistency of the soil, by which occurrence of pocket gophers is determined in Berkeley, California. And he concludes: "The ecologic niche of this animal is therefore comprised within the terrain that provides these special features of environment."

"No two species in the same general territory can occupy for long identically the same ecologic niche. If, by chance, the vagaries of distributional movement result in introducing into a new territory the *ecologic homologue* (italics mine) of a species already endemic in that territory, competitive displacement of one of the species by the other is bound to take place. Perfect balance is inconceivable" (Grinnell 1928/1943: 192-194).

Upon reading these four papers it is clear that although niche is literally classified under habitat, he means it to be the ultimate unit within an association, *i.e.* within a biotic community, but not of a spatial nature. By the same reasoning, although he also discusses faunas in the same sentence relating to classification of habitats (1924 *l.c.*), we would not think that Grinnell calls a fauna a habitat.[1]

We also note that in 1928 Grinnell emphasized food and enemies as two critical factors in comprising the pocket gopher's niche. Elton's (1927) definition explicitly hinges on these two factors: ". . . the 'niche' of an animal means its place [sic!] in the biotic environment, *its relation to food and enemies*" (Elton's italics).

The *ecological niche,* then, in agreement with both Grinnell's and Elton's concepts, is a functional entity within the biotic community which can be studied in a comparative way. It can be demonstrated easiest by the presence of an occupant species (*cf.* Udvardy 1957: 310). Geographically separated but structurally related and similar biotopes, with similar biotic communities, may provide similar or even identical niches. When these are filled with taxonomically different animal occupants, these animals often show far going similarities in functional adaptations as results of parallel or convergent evolution. Niches, as Grinnell several times pointed out, are subjects of evolution and they, in turn, are governing factors of evolution for their occupants.

The study of ecological counterparts—the ecological homologues of Grinnell—seems to me to be a promising approach for an understanding of environmental and distributional relations of animals. In continental Europe they are called *"life forms."* According to Tischler (1949) Remane (1943) is credited with the use of this concept, classifying life forms according to locomotion, feeding and physical environmental strata.

Now let us consider "Gause's law" (Savage 1958), or "Gause's hypothesis" (*cf.* Gilbert *et al.* 1952) which states that "as a result of competition two similar species scarcely ever occupy similar niches" (Gause 1934: 19). With all due respect for Gause's demonstrative experiments on this subject, the concept should justly be called *Grinnell's axiom* (see quotations above, Grinnell 1904, *1917*, 1928). It has been pointed out several times that ecological diversification is not necessarily the result of direct and active competition (Birch 1957, Gilbert, Reynoldson and Hobart 1952, Udvardy 1951). Moreover, since the definition of a niche (whether we take that of Grinnell, Elton, Gause, or anyone else) does not specify the number of essential factors or relations that compose the niche, there seldom will be an occasion to prove that two suspected species occupy exactly the same one. A differentiating factor is usually found when scrutinizing the ecology of the supposed co-occupants (for details see Hutchinson 1957). The study by Ross (1957) of three species of leafhoppers with "identical" niche requirements seems to provide a practical example contradicting the validity of "Gause's hypothesis" but not opposing Grinnell's axiom, since Grinnell, rightly, includes the phrases: "evenly balanced" (1904) and "for long" (1928). Since environments and niches are not stable, evolutionally speaking, but themselves are subject to evolutionary changes (Grinnell 1924, *l.c.*), these leafhoppers, or any other animals apparently coexisting in a niche, may never be subjects of the Volterra-Gause principle (*sensu* Hutchinson 1957), because their ecoexistence is almost certainly temporary.

---

[1] Besides developing the niche concept, and the axiom of incompatibility in sharing niches, Grinnell here also states clearly the essentials of several such ecological principles that became noted, and elaborated upon, much later and by other biologists. These are: the principle that in ecological speciation the essential is geographical isolation (Grinnell 1904: 372, later Mayr, 1942 etc.); that food is the density dependent factor that regulates the numbers of animals (Grinnell 1904; later Lack 1954); that birds actively select their habitats (Grinnell 1917B, later Lack 1933).

In conclusion I should like to emphasize that habitat and ecological niche are related concepts in different approaches of study. The first is an idiobiological abstraction used when considering a species *per se;* the second is a product of synecological thinking. There seems no essential difference between the niche concept of Grinnell and of Elton. Grinnell's formulation is prior, broader, and approaches the general usage of the term. Therefore I recommend it for general acceptance. Grinnell's axiom, as stated in 1917 (*l.c.*) and 1928 (*l.c.*) antedates Gause's statement about similar species scarcely ever occupying similar niches. It is so formulated that it seems to circumvent the criticisms raised against the practical validity of Gause's statement.

It is recommended that attention of ecologists be focused on the concept of "life forms," meaning in animal studies a system of functionally related ecological counterparts. Their study may clarify many aspects of animal ecology and distributional geography.

The concept of biotope belongs to the realm of synecology. It is a convenient term for the habitat of a biotic community. This usage should be encouraged, and certain misuse (as a synonym for habitat proper) should be eliminated.

I am indebted for stimulating discussions and advice to R. W. Hiatt, S. J. Townsley, and the participants of the Cold Spring Harbor Symposium on Quantitative Biology in June 1957.

References

Birch, L. C. 1957. The meanings of competition. Amer. Naturalist **91:** 5-18.

Carpenter, J. R. 1938. An ecological glossary. Norman; Univ. of Oklahoma Press.

Clements, F. E. and V. E. Shelford. 1939. Bio-Ecology. New York; Wiley.

Dahl, F. 1908. Grundsätze und Grundbegriffe der biocönotischen Forschung. Zool. Anz. **33:** 349-353.

Dice, L. R. 1952. Natural Communities. Ann Arbor; Univ. of Michigan Press.

Elton, C. S. 1927. Animal Ecology. London; Sidgwick and Jackson.

Friederichs, K. 1927. Grundsätzliches über die Lebenseiheiten höherer Ordnung und den ökologischen Einheitsfaktor. Die Naturwiss. **15:** 153-157, 182-186.

———. 1958. A definition of ecology and some thoughts about basic concepts. Ecology **39:** 154-159.

Gause, G. F. 1934. The Struggle for Existence. Baltimore; Williams and Wilkins.

Gilbert, O., T. B. Reynoldson and J. Hobart. 1952. Gause's hypothesis; an examination. Jour. Anim. Ecol. **21:** 310-312.

Grinnell, J. 1904. The origin and distribution of the chestnut-backed chickadee. Auk **21:** 364-382.

———. 1917. A. The niche-relationships of the California thrasher. Auk **34:** 427-433.

———. 1917. B. Field tests of theories concerning distributional control. Amer. Naturalist **51:** 115-128.

———. 1924. Geography and evolution. Ecology **5:** 225-229.

———. 1928. The presence and absence of animals. Univ. Calif. Chronicle **30:** 429-450. Read as reprinted in: Joseph Grinnell's Philosophy of Nature. Berkeley 1943. Pp. 187-208.

Heinrich, G. 1958. Zur Verbreitung und Lebensweise der Vögel von Angola. Systematischer Teil III. J. Orn. **99:** 399-421.

Hesse, R. 1924. Tiergeographie auf ökologische Grundlage. Jena; Fischer.

———, **W. C. Allee and K. Schmidt.** 1937. Ecological Animal Geography. New York; Wiley.

Hoesch, W. 1958. Nest und Gelege der Wüstenlerche. J. Orn. **99:** 426-430.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. **22:** 415-427.

Lack, D. 1933. Habitat selection in birds. J. Anim. Ecol. **2:** 239-262.

———. 1954. The Natural Regulation of Animal Numbers. Oxford; Clarendon.

Mayr, E. 1942. Systematics and the Origin of Species. New York; Columbia Univ. Press.

Odum, E. P. 1953. Fundamentals of Ecology. Philadelphia; Saunders.

Palmgren, P. 1930. Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands. Acta Zool. Fennica **7.** Helsinki.

Petersen, C. G. J. 1915. Om Havbundens dyresamfund i Skagerak, Kristianiafjord og de danske Farvande. Beretning t. Landbruksministeriet fra Den danske biologiske Station **23:** 1-26.

Peterson, R., G. Mountfort, P. A. D. Hollom and C.-F. Lundevall. 1955. Europas fåglar. Stockholm.

Remane, A. 1943. Die Bedeutung der Lebensformtypen für die Ökologie. Biol. Generalis **17:** 164-182.

Ross, H. H. 1957. Principles of natural coexistence indicated by leaf-hopper populations. Evolution **11:** 113-129.

———. 1958. Further comments on niches and natural coexistence. Evolution **12:** 112-113.

Savage, J. M. 1958. The concept of ecologic niche, with reference to the theory of natural coexistence. Evolution **12:** 111-112.

Svärdson, G. 1949. Competition and habitat selection in birds. Oikos **1**: 157-174.

Tischler, W. 1949. Grundzüge der terrestrischen Tierökologi. Braunschweig.

Udvardy, M. D. F. 1951. The significance of interspecific competition in bird life. Oikos **3**: 98-123.

———. 1957. An evaluation of quantitative studies in birds. Cold Spring Harbor Symp. Quant. Biol. **22**: 301-311.

MIKLOS F. D. UDVARDY

UNIVERSITY OF BRITISH COLUMBIA,
VANCOUVER, B. C., CANADA; AND
UNIVERSITY OF HAWAII,
HONOLULU, HAWAII, USA.

A NOTE ON SHOCK DISEASE

This paper reviews the evidence presented by the late Dr. R. G. Green and his colleagues about the nature of "shock disease," a pathological condition believed to have been associated with a decline in numbers of the snowshoe hare (*Lepus americanus*). The original impetus for this review came from my own failure to find a similar condition among natural populations of the vole, *Microtus agrestis,* and the discovery that low glycogen reserves were not necessarily accompanied by poor survival in experimental populations in the laboratory. Failure to discover shock diseases in voles does not, of course, imply that it does not occur in snowshoe hares; but if wild hares do not get shock disease there is no reason to expect it in voles. Before going on with a line of research that had apparently led nowhere it therefore seemed advisable to see if the original evidence really had shown that wild hares were decimated by such a disease.

It soon became obvious that the data were inadequate to support the belief that "shock disease is responsible for the die-off of the snowshoe hare throughout its range in North America" (Green, Larson and Bell 1939). Among the difficulties of accepting this hypothesis is the conclusion of Green and Evans (1940), on the one hand, that mortality among the adult and yearling hares had not "varied enough to be of major importance as a cause of the cycle," whereas Green, Larson and Bell (1939), referring to the same age groups, "found shock disease to involve almost the entire hare population." I therefore re-examined the whole of the evidence, and here try to show how the authors reached their conclusions, and why I myself am doubtful about some of them. Except in the case of direct quotations I have mostly omitted individual references.

PUBLISHED CONCLUSIONS

The authors reached the following conclusions about changes in the numbers of a natural population of snowshoe hares in Minnesota: (1) a decline in total numbers was spread over the five consecutive years 1933-8 (2) the decline was not obviously associated with emigration, food shortage, reduced fecundity, infectious disease, parasitism, or predation (3) animals which survived until the autumn of their first year of life died off thereafter at an annual rate which remained approximately constant from 1933-9, except for a particularly high death-rate among the rather low population of 1937-8 (4) mortality among these adults and yearlings was obviously not the principal cause of the decline, and (5) the 5-year decline in total numbers was a consequence of a high juvenile death-rate among the hares calculated to have been born in 1933-7, the greater part of the loss probably occurring during their first few weeks of life.

As some of these conclusions are based on data obtained by capture-recapture methods they involve assumptions which, if false, can lead to serious errors (*e.g.* if marked and unmarked animals are not equally at risk of capture); but I shall here assume that we may accept the qualitative accuracy of the conclusions given above from Green and Evans (1940), even though numerical values, such as those used in Tables I and II, may be biased. I shall also accept the authors' assumption that their detailed population study was a fair sample of events in all areas, including those from which they received many of the animals examined.

Two further conclusions were these (Green and Larson 1938 a & b; Green, Larson and Bell 1939): (6) during the period of the decline most of the animals were in an abnormal condition which predisposed them, although in apparently good health, to die suddenly under physical or nervous stress, and (7) this predisposing condition (shock disease) was characterized by degeneration of the liver, failure to store glycogen, and a low blood sugar level; death occurred from hypoglycemic shock.

The present paper does not deny that a pathological condition of some sort was present in the wild population; or that cytoplasmic degeneration of the liver accompanied an abnormal death-rate in captivity; but it gives reason for doubting if the latter condition helps to explain what was going on in the wild. Even if these doubts are justified they do not, of course, detract from the main value of the work on the snowshoe hare. Not only was this a pioneer attempt to solve a problem which is still unsolved, but it provided unique data on mortality rates, reduced the plausibility of existing interpretations of them, and offered the alternative hypothesis that there had been a change in physiological condition.

NATURE OF THE EVIDENCE

The argument that shock disease was the factor primarily responsible for the decline in numbers rests upon the following evidence:

(a) Large numbers of hares died in the wild during 1936
(b) Hares kept together indoors in the spring of 1936 died at a high rate with certain characteristic terminal symptoms
(c) A higher proportion of hares died in the traps in 1936 than in the two previous years
(d) A population breeding in an outdoor enclosure declined in numbers in 1936
(e) The symptoms of death in nature, in captivity, and in the traps were alike; it could therefore be assumed that the primary cause of death was the same in all instances.

Stated in this manner the evidence forms a consistent, and at first sight convincing pattern. However, the writers of the papers published in 1938-9, about shock disease in adults and yearlings, seem to have been unaware, or at least do not mention that it was only the juvenile death-rate that was responsible for the population decline (except in 1937-8). From the later analysis of Green and Evans (1940) it now seems clear that the factors killing the adults and yearlings in captivity were absent from the wild or were having no measurably different effect from year to year.

Shipments of hares

Hares, sent by rail from various areas in Wisconsin and Minnesota, were received on different dates in March and April 1936. On arrival the survivors were put into a room 560 sq. ft. in area. Nearly all animals died within three weeks, some abruptly, others after symptoms lasting several hours, including severe convulsions. Blood samples were taken from the heart at various times before death and soon after; necropsies were performed as soon as possible after death. Green and Larson (1938a) state that captivity involved only a "mild but continuous strain." The term "mild" is scarcely appropriate, however, as none of the animals in the three largest groups lived more than 20 days, whereas one-third of those at liberty were still alive a year later (Table I).

TABLE I. Percentage of animals dying on the whole area: adults since the previous Feb., young since birth in the previous summer

Feb.	1933	1934	1935	1936	1937	1938	1939
Adults and yearlings	approx. 70%				64	97	59
Young	<53	77	71	82	88	92	9

Biochemical findings were as follows: (a) Among two groups of captive hares killed while apparently normal one group had liver glycogen contents of 1.2-12%, the other group had $< 1\%$ glycogen and was said to be in "pre-shock" condition. Blood sugar contents were similar in both groups (averages respectively 134 and 141 mg per 100 cc.). (b) Among hares which were dying in coma "rather large" numbers had normal or increased blood sugar levels; but most had low levels which it was difficult to raise and maintain by injections of glucose. Although symptoms of shock were markedly relieved, death could not be prevented, and the animals injected lived little longer than those which were not. (c) Among hares that had actually died of shock disease liver glycogen contents were low in each of 7 animals, blood sugar levels were also low except in one case.

Thus the symptoms associated with morbidity and death from shock disease include low levels of liver glycogen; low, normal or high levels of blood sugar; rapid or prolonged death agonies.

Until Nov. 1935 hares had been kept in limited spaces and had suffered negligible mortality, but no evidence is given to show that procedures were strictly comparable to those of 1936. Indeed, since the number of hares previously kept together had almost certainly been far less, the high death-rate in 1936 may simply reflect unfavourable conditions associated with gross overcrowding. For example there were 48 live hares in the first shipment, and 90 in the second, which arrived two days later and was added to the survivors from the first. The low average survival time of about 4 days was accepted as evidence that a change in viability had occurred in the animals before they were captured. Such a conclusion is unjustified, however, because of the absence of data for control groups of animals subjected to identical conditions of transport and crowding at the same time of year. By 1936, unfortunately, there were no expanding populations to provide samples for simultaneous controls; and without comparable data from previous years (or for isolated animals in 1936) there is no evidence against the alternative views that overcrowding alone was sufficient to account for the abnormal death-rate, or that the hares were less mutually tolerant than in previous years. It is otherwise hard to account for the poor survival in captivity in 1936, since there had been no change in viability in the wild. It is also hard to account for the good survival in captivity in 1937, if it is true that shock disease continued to kill off the wild hares until 1938; but if allowance is made for the small numbers in captivity it is possible to understand why they did not develop shock disease. The conflict of evidence is shown in the following quotations from Green and others (1933-9).

January 1937. "Evidence that shock disease is declining in severity in the hare populations of this state has been apparent in the past month. The change was first noticed in autopsying animals. The lesions characteristically attendant on this disease were present in a lesser degree in the specimens received at the laboratories. This fact was observed during the period when captive hares exhibited an ability to survive for long periods without presenting the symptoms of shock disease so ubiquitous in the hares captured in the spring of 1936."

February 1937. "Data collected during February substantiated previously accumulated evidence that shock disease is declining in severity. This downward trend is in progress at a time of year when the disease was at its height in 1936."

April 1938. ". . . the mortality factor which last year had reduced the number of snowshoe hares to about one-third of peak population, has continued with undiminished severity to force the population downward."

Trap-deaths

Trapping was largely confined to the non-breeding season *i.e.* after the severe juvenile mortality had ceased and when the catch consisted of adults, and yearlings which by then were subject to an adult death-rate. The percentage of individuals dying in the traps, and its relation to the estimated changes in population density (Table II), were believed to provide evidence about the natural occurrence of shock disease. The high precentages of trap-deaths at the start of operations (5.3 and 13.9% on the two parts of the area) were said to be largely explained by an accumulation of hares with shock disease, and the authors attach less significance to these high figures during the increase in numbers than to the figures of 3.7 and 8.6% observed during the decline in 1936. Also, in 1934 and 1935 there was a higher death-rate on the Square Mile, where numbers were not decreasing, than on the rest of the area where they were. Thus in order to relate the proportion of trap-deaths to the population decline it is necessary to explain away the fact that the highest figures in both areas occurred during periods of increase, and to attach special significance to those for 1936. It is also necessary to disregard the fact that the trap-deaths occurred among adults and yearlings, for which the death-rate in nature remained constant until 1937-8. It thus seems more probable that trap-deaths merely reflect variations in the intensity of trapping, handling, and other procedures.

TABLE II. Relation of trap-deaths to population trends (Relative population density is given as a multiple of that estimated for the previous February)

	1932	1933	1934	1935	1936	1937	1938	1939
				(a) *Whole area*				
Population density per sq. mile....	c.275	478	374	356	246	151	32	73
				(b) *The Square Mile (intensively trapped)*†				
Relative population density...	>1.0	>1.0	1.02	1.07	0.58	0.53	0.33	1.67
% trap-deaths....	—	13.9	4.3	4.9	8.6	8.6	7.0	
				(c) *Area exclusive of the Square Mile*				
Relative population density...	>1.0	c.1.7*	0.70	0.81	0.76	0.65	0.17	2.28*
% trap-deaths....	5.3	4.8	1.1	1.4	3.7	1.6	(11.1)‡	

* including the Square Mile.
† especially from fall 1935
‡ Only 9 animals trapped.

Atrophy of the liver

Toxic cytoplasmic degeneration was found in sections cut from the livers of trapped or captive animals found dead, or observed to die with symptoms of shock disease. The gross appearance of their livers is described as follows: "Usually in advanced cases the liver is a dark mahogany in color and is atrophic and definitely smaller than normal, so that the capsule is separated from the parenchyma and lies as a wrinkled membrane over the surface of the organ" (Green and Larson 1938a). In addition: "A sweet, nauseating odor was perceptible upon opening the abdominal cavity of hares dying of shock" (Green and Larson 1938b).

Hares suffering from shock disease appeared normal until they developed convulsions; nevertheless their average weight was 225 g (16%) less than those which were shot, or survived being trapped. This loss in body weight was attributed to the effects of shock disease on carbohydrate metabolism; but a simpler explanation is that, as in other species of wild animals, some individuals lose weight in captivity and become further dehydrated after death.

The most advanced lesions were infrequent until 1936, and "as the die-off abated, the severity of the lesions again decreased" (Green and Larson 1938b). Now the death-rate of the adults and yearlings was no higher in 1936 than in previous years and much lower than in 1937-8, which is the latest period to which these authors can be referring in a paper submitted in May 1938. Apparently then, symptoms of shock disease not only became more severe in 1936 when there was no change in the death-rate, but became less severe afterwards when the death-rate increased.

An outdoor enclosure

In the spring of 1936 forty-one adult females and 6 males were put into a fenced area of 1.7 acres, 4 more males being added later. Additional food was provided each day. Twenty-three adults were still alive in November, but only 8 out of their 115 young, of which 82 corpses were examined. The majority of deaths were attributed to shock disease, chiefly because of the peculiar liver degeneration present in advanced cases, and because of the way some of the hares died:

"The occurrence of shock disease in young hares was rigidly demonstrated by studies on hare No. 4237. This animal was born on May 6, 1936. On July 1 it was captured in order that a sample of blood might be taken. Its blood sugar level was normal. The hare was returned to the range, and at 9:30 the following morning was found huddled up, indifferent to the approach of an observer. At 11:15 it was lying on its side, too weak to assume a normal posture, and when picked up and carried into the laboratory, it developed convulsions. Its blood contained 3 mg sugar per 100 cc. This hare, born in the range and living under essentially natural conditions, died from shock disease 57 days after birth.

"Many young hares that had never been handled except during the brief process of ear-banding, died of shock disease . . ." (Green, Mather and Larson 1938).

This evidence shows that shock disease could not be recognized from a blood sugar determination until the animal was obviously dying.

It may be that the mortality factors associated with this high juvenile death-rate were the same as those in nature; but there is not enough evidence to decide this point, as the amount of natural cover and other conditions in the enclosure may have been different from those in nature. Also the population was established from an arbitrary assemblage of animals at an unnaturally high adult density for this part of the country (about 18,000 per sq. mile), and in terms of females the discrepancy was much greater. Fighting among captive animals is frequently referred to in the mimeographed reports, and presumably contributed to the death-rate of these animals.

Shock disease in the wild

There is comparatively little evidence that most of the wild animals died of shock disease rather than of something else: terminal symptoms that may either be abrupt or last up to 3 days, are not by themselves diagnostic. An occasional hare was found in a position which indicated that it had died suddenly; some were seen dying suddenly; one died in convulsions lasting over 75 min., and the "pathological findings were definitely diagnostic of shock disease" (Green, Larson, and Mather 1938). Other animals found dead in the wild also had the same histopathology as those dying in captivity. However, shock disease does not seem to have been recognized in any random sample obtained in such a manner as to preclude the possibility that the methods of capture and treatment were sufficient to account for any changes in physiological state. Nor are any abnormalities described in the numerous hares shot or trapped for pregnancy determinations and other purposes. There is therefore insufficient evidence to justify the view that there was a common cause of death (as opposed to common terminal symptoms) among the adults and yearlings in the traps, and in captivity indoors, and among all age groups in the enclosure and in the wild.

REVISED CONCLUSIONS

The only evidence about the nature of the condition in the young is that they did not survive in the outdoor enclosure, that liver degeneration was found *post mortem*, and that a hare on the point of death had a low blood sugar level. The evidence is more extensive in the case of the captive adults and yearlings, but bears no relation to anything recorded about these age groups in nature. Except for a sharp increase in 1937-8 their death-rate remained approximately constant and was apparently not the significant factor associated with the decline in population density. In the traps, however, their death-rate varied from year to year, lesions of the liver were noticeably common in 1936 only, and the abnormally high death-rate in captivity also took place in 1936 without any corresponding change in the death-rate in nature.

It therefore seems to be the case that the authors have studied at least two main phenomena. They have shown that hares died when removed from the wild just before the breeding season and kept at high densities in a small room or an outdoor enclosure, while similar animals were viable in their natural habitat. The other main set of facts is that the wild populations continued to have an abnormally low rate of recruitment for 5 consecutive years. The assumption is then made that these non-viable young in nature were afflicted with a condition identical with the one that killed adults and yearlings indoors, and all age groups in the outdoor enclosure. The purpose of the present paper has been to show that, whatever the facts about shock disease among captive animals, no such condition has yet been shown to explain the progressive increase in juvenile death-rate with decreasing population density in nature.

There is no evidence of, nor any need to postulate an abnormal predisposing condition among the hares that died in the traps and captivity. It is by no means unusual for wild animals to die during trapping, transport, and confinement, especially if they are kept in groups, and cellular changes may be expected in any animal that succumbs to rough treatment of this sort. This interpretation can be tested by seeing whether shock disease can be produced experimentally by overcrowding, and whether the same cytological changes occur in the livers of animals dying under various other adverse circumstances in the laboratory and in nature.

Acknowledgments

I am greatly indebted to Dr. E. W. Fager for many long discussions and much practical help, but he should not be blamed for any errors I may have made in trying to reinterpret these important studies. I am also grateful to Dr. A. H. T. Robb-Smith and several other people for useful comments. The final form of this paper owes much to correspondence and discussion with Dr. J. Frederick Bell and Dr. Carl L. Larson (who collaborated with the late Dr. Robert Green on the laboratory work) and with Dr. Charles A. Evans (who analyzed the field results). Although we are at present unconvinced by each others' arguments we agree that the issues can be decided only by further work. Dr. Bell writes: "We cannot credit your implication that the extensive lesions of the liver developed while the animal was in a trap or during a short period in captivity." I nevertheless hope I have made out a case for taking this implication seriously.

Summary

1. It was concluded by Green and Evans (1940) that an abnormally high death-rate among the juveniles was the principal factor leading to a decline in the numbers of the snowshoe hare (*Lepus americanus*).

2. Observations were made on adult and yearling hares dying under crowded conditions in the laboratory, or on those that had died in the traps (Green and Larson 1938a & b; Green, Larson and Bell 1939). The corpses of 82 young hares which had died in an outdoor enclosure were also examined (Green, Larson and Mather 1938; Green, Mather and Larson 1938). No published data are available for animals taken from the wild in such a manner that their physiological condition could not have been affected by capture, confinement, or death; nevertheless a condition termed "shock disease" was claimed to be prevalent among all age groups in nature.

3. Shock disease was recognizable only in dead or moribund animals, and although its terminal symptoms were mostly non-specific, the condition was diagnosed from gross and microscopic lesions of the liver.

4. The incidence of abnormalities among captive hares bore no relation to changes in the density of the wild populations: (a) the proportion of animals dying in the traps was highest at times when the natural death-rate was lowest (b) adults and yearlings died within 3 weeks when brought into the laboratory in 1936, but survived perfectly well in 1937, although the natural death-rate remained constant at about 70% per annum (c) advanced lesions of the liver had become less common by 1938 although the natural death-rate had risen to an estimated 97%.

5. There is thus no evidence of a naturally occurring change in the predisposition of these wild animals to die when treated unsuitably enough after capture. Shock disease is perhaps a less specific condition than has been claimed, in which case its symptoms, including rapid morphological changes in the liver, are to be expected in animals dying in convulsions under various kinds of adverse circumstances.

6. If we accept the field evidence that the adult death-rate was normal, we cannot accept the inference that it was abnormal owing to the ravages of shock disease; nor is there any evidence that shock disease was associated with the abnormal juvenile mortality.

References

Green, R. G. and C. A. Evans. 1940. Studies on a population cycle of snowshoe hares on the Lake Alexander Area. . . . J. Wildlife Man. **4:** 220-238, 267-278, 347-358.

*———, ———, **and C. L. Larson.** 1943. A ten year population study of the rabbit tick *Haemaphysalis leporis-palustris.* Amer. J. Hyg. **38:** 260-281.

———, **and C. L. Larson.** 1938a. Shock disease and the snowshoe hare cycle. Science **87:** 298-299.

——— **and C. L. Larson.** 1938b. A description of shock disease in the snowshoe hare. Amer. J. Hyg. **28:** 190-212.

———, ———, **and J. F. Bell.** 1939. Shock disease as the cause of the periodical decimation of the snowshoe hare. Amer. J. Hyg. **30B:** 83-102.

———, ———, **and D. W. Mather.** 1938. The natural occurrence of shock disease in hares. Trans. 3rd N. Amer. Wildlife Conf. 877-881.

———, **D. W. Mather, and C. L. Larson.** 1938. Occurrence of shock disease among young snowshoe hares. Proc. Soc. Exp. Biol., N.Y. **38:** 816-817.

——— **and others** [1933-39]. Minnesota Wildlife Disease Investigation. Mimeographed reports, Vol. 1-4.

Dennis Chitty

Bureau of Animal Population
Department of Zoological Field Studies
Oxford University

---

* This paper, which is not referred to in the present text, contains much additional information.

THE ESTIMATION OF DENSITY OF *CONVOLVULUS ARVENSIS* IN A GRASS-LEGUME MIXTURE

The plant sociologists determine the quantitative characteristics of a community by subjective estimation (Braun-Blanquet 1928). To work with objectivity, we need to find some way by which we can characterize the density and distribution of a certain species within the community. We can estimate the number of individuals per unit area. To illustrate the variability of numbers, the Poisson law of frequency and Neyman's contagious distribution of type A and other frequency distributions are often used (Archibald 1948, Barnes and Stanbury 1951, Neyman 1939, Weber 1957). The size and the spatial relation of the sample are important for estimating the parameters of these distributions. Hence examples based on data from a relatively uniform or known population have an interesting bearing on quantitative ecological sampling in general.

The observed data was sampled from a plot with 25 m² which was shown with a mixture of *Dactylis glomerata* and *Lotus corniculatus.* The number of individuals of Convolvulus was determined in adjacent subdivisions of the plot, of varying sizes (5 x 100 cm, 10 x 100 cm, 25 x 100 cm, 50 x 100 cm and 100 x 100 cm). For plots by 500 cm² the mean of .296 was first used to calculate expected values for the number of plots with 0, 1, 2, and 3 individuals according to the Poisson distribution by substituting $\bar{x}$ for λ in the formula:

$$P_{n.k} = e^{-\lambda} \frac{\lambda^k}{k!} \qquad (1)$$

For the Neyman distribution of type A expected values were calculated by the formula:

$$P(X = k+1) = \frac{m_1 m_2 e^{-m_2}}{k+1} \sum_{t=0}^{k} \frac{m_2^{\,t}}{t!} P(X = k-t), \qquad (2)$$

$$m_2 = \frac{\mu_2 - \mu'_1}{\mu'_2}, \quad m_1 = \frac{\mu'_1}{m_2};$$

$$\mu'_1 = \bar{x} \qquad \text{and } \mu_2 = s^2.$$

From Table I it is apparent that over the quadrat area of 2500 cm² the Neyman distribution does not give a real approximation, but under this area it gives a very good approach. In other words the Neyman distribution is reliable if the area of the observation quadrat (subplot) is smaller than 1/100 of the whole experimental field.

TABLE I. Values observed and calculated by the Poisson distribution and the Neyman Contagious distribution of type A for varying sizes of subplots

Size of subplot	500 cm²			1000 cm²			2500 cm²		
No. of individuals per subplots	O.*	P.	N.	O.	P.	N.	O.	P.	N.
0	382	372.65	381.70	152	138.57	149.82	37	22.76	39.45
1	93	110.30	94.70	63	82.03	65.93	27	33.68	21.05
2	20	16.32	24.21	23	24.28	24.28	14	24.93	16.35
3	5	1.61	4.68	10	4.78	6.88	10	12.29	8.43
4				1	.71	1.94	4	4.55	5.74
5				1	.08	.28	3	1.34	4.73
6							3	.33	2.93
7							2	.07	1.65
N =	500			250			100		
$\lambda =$		.296			.592			1.48	
$s^2 =$		.349			.7695			2.989	
$P_{\chi^2} =$		<.01	.5–.3		<.1	≈.2		<.01	≈.3

Size of subplot	5000 cm²			10,000 cm²		
No. of individuals per subplots	O.	P.	N.	O.	P.	N.
0	1	2.59	—	0	0.07	—
1	6	7.67	—	0	.40	—
2	16	9.81	—	1	1.18	—
3	14	9.67	—	2	2.33	—
4	6	7.16	—	3	3.45	—
5	2	4.24	—	5	4.07	—
6	2	2.03	—	6	4.01	—
7	2	.88	—	2	3.39	—
8	1	.33	—	3	2.51	—
9				1	1.65	—
10				2	.97	—
N =	50			25		
$x =$		2.96			5.92	
$s^2 =$		2.81			4.41	
$P_{\chi^2} =$		0.1–.05			.5–.3	

* O. = observed frequency.
P. = frequency calculated by Poisson distribution.
N. = frequency calculated by Neyman distribution.

REFERENCES

Archibald, E. E. A. 1948. Plant populations. I. A new application of Neyman's contagious distribution. Ann. Bot. N.S. 12: 221.

Barnes, H. and F. A. Stanbury. 1951. A statistical study of plant distribution during the colonization and early development on china clay residues. Jour. Ecology 39: 171.

Braun-Blanquet, J. 1928. Pflanzensoziologie. Berlin.

Neyman, J. 1939. On a new class of "contagious" distributions, applicable in entomology and bacteriology. Ann. Math. Stat. 10: 35.

Weber, E. 1957. Gundriss der biologischen Statistik. Jena.

S. PRÉCSÉNYI

ON THE SPONTANEOUS GROWTH OF *PSEUDOCOCCOMYXA ADHAERENS* (CHLOROPHYCEAE) IN CHEMICAL SOLUTIONS

In the chemical laboratories of the Department of Water Technology, Prague, Czechoslovakia, a remarkable phenomenon was observed. The bottom of some flasks with chemical solutions prepared for analytical purposes became covered with a homogenous green layer. In the winter months of 1957-1958 the growth occurred in the 0.01 N KCl-solution. The flask was kept near an electric lamp in the laboratory. After microscopic analysis of the layer, I determined it as the unicellular green alga *Pseudococcomyxa adhaerens* Korshikov 1953 (Fig. 1). Because the occurrence of an alga in KCl-solution is rather unusual, I tried subsequently to inoculate this alga into the ten times more concentrated solution, i.e. 0.1 N KCl. The inoculum was obtained by means of centrifugation of the disturbed solution from the original flask. The flask with 0.1 N KCl was placed under similar laboratory conditions. After a few months a thin light greenish layer began to form and over a period of several months it grew and covered the entire bottom. The microscopic examination showed that the cells were filled with volutin and oil drops and the chromatophores were pale and often separated into fragments of irregular shape (Fig. 1(4)). Furthermore, the size of cells was smaller in comparison with the state in the 0.01 N KCl-solution (Fig. 1(3)). It is evident that the 0.1 N KCl-solution is not a suitable environment for this green alga. At the same time another green layer consisting of the same organism formed spontaneously in the M/15 solution of KH_2PO_4. The cells in this flask were well developed: they formed many autospores and their chromatophores were bright green.

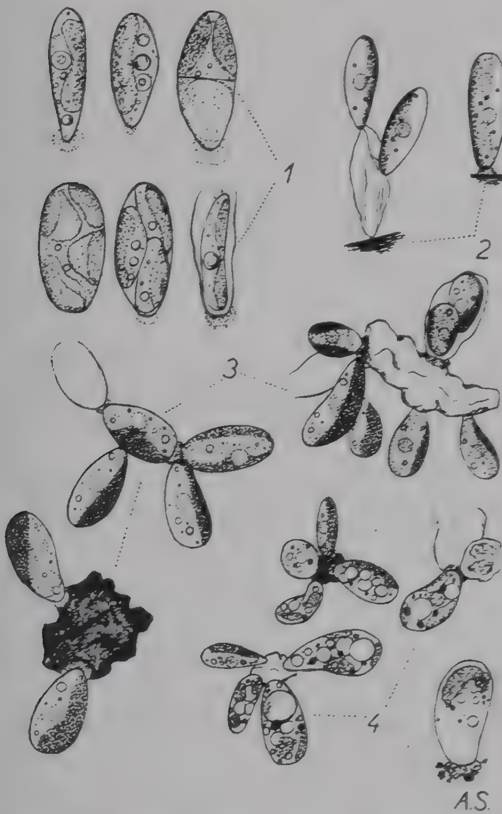


FIG. 1. *Pseudococcomyxa adhaerens* Korshikov. (1) from Korshikov, redrawn and reduced. (2) Two of the 9 figures of Fott and Komárek, redrawn and reduced. One typical cell adhering to the substratum with a little gelatinous heap and two cells attached to the empty membrane of the mother cell. (3) General view of *Pseudococcomyxa adhaerens* in 0.01 N KCl-solution. The cells are attached to detritus particles or form *Saccharomyces*-like chains. Dimensions of cells: 4.5-10.5 μ x 2.5-5 μ. (4) The cells from 0.1 N KCl solution. They contain many large oil and volutin drops and their chromatophores are separated into irregular pieces. Dimensions of cells: 6-9 x 2-5 μ. (3) and (4) are originals.

Pseudococcomyxa adhaerens belongs to Protococcales and was described 1953 by O. A. Korshikov (=Korschikoff = Koršikov) from the vicinity of Kharkov in Ukraine (Fig. 1(1)). Under natural conditions no mass development was observed but in cultures it grew very well. B. Fott and J. Komárek 1958 found this alga also in chemical solutions in the laboratory of the Botanical Institute in Prague (Fig. 1(2)). The authors did not give exactly either the sort of solutions or their concentration; they stated only that the solutions were the stock for the preparation of algal nutrient media. Because the article was taxonomic in nature, the authors translated into German the original Ukrainian diagnosis of Korshikov and added several new notions. They isolated this alga from the solutions and they maintained it in agar culture. The ecological statements in this article are in accordance with my own observations. The same manner of growth, i.e. the formation of layers on the bottom of flasks and the accumulation of cells around detritus particles, was observed. As in my KCl solutions, the formation of *Saccharomyces*-like chains was noted (Fig. 1(3)). The attachment of cells to the surface film of the solution, as found by Korshikov, was not observed in any case.

It is suggested that culture of unicellular algae at varying concentrations of nutrient, both in unialgal culture as well as in culture with other competing unicells, would serve to reveal many useful facts about the ecology of each algal species. Many such algae are found only rarely in nature because they are usually suppressed when they live among vigorous competitors. But under unusual conditions such as those of the chemical solutions described here, the majority of algae and coexisting organisms is excluded and algae with limited nutrient requirements and great adaptabiilty can grow massively.

SUMMARY

The green alga *Pseudoccomyxa adhaerens* Korshikov appeared spontaneously in mass development as a green layer on the bottom of flasks containing the solutions of 0.01 KCl and M/15 KH_2PO_4. It grew also in the 0.1 N KCl-solution after inoculation, but the cells were smaller and degenerated.

The occurrence of this alga was discussed with respect to the fact that it was described in 1953 by O. A. Korshikov from Ukraine, found later by B. Fott and J. Komárek (1958) in Czechoslovakia also in similar unusual environment, in different chemical solutions than in my case.

Further ecological studies of this interesting alga are recommended.

REFERENCES

Fott, B. 1956. Sinice a řasy. (Blue-green Algae and Algae. In Czech.) 373 pp. Czechoslovak Academy of Science Press. (German translation "Algenkunde", in press.)

Fott, B. 1958. Personal communication.

Fott, B. and J. Komárek. 1958. Über eine häufig übersehene Grünalge: *Pseudococcomyxa adhaerens* Koršikov. Preslia **30**: 76-77.

Korshikov, O. A. 1953. Viznačnik prisnovodnich vodorostej Ukrainskoj RSR. Pidklass Protokokkovi (Protococcineae). 436 p. Kiiv.

ALENA SLÁDEČKOVÁ
DEPARTMENT OF WATER TECHNOLOGY
INSTITUTE OF CHEMICAL TECHNOLOGY
TROJANOVA 13, PRAHA 2, CZECHOSLOVAKIA

INTERACTION OF SPECIES AND SOIL IN RELATION TO THE DISTRIBUTION OF EUCALYPTS

Field observations in the Southern Tablelands Region of New South Wales and elsewhere have suggested that the distribution of the Eucalypts is frequently edaphically controlled. Experimental work by the author (Moore 1959) aimed at determining the soil factors involved has indicated that significant differences in the nutrient status of the soils of neighboring, sharply defined communities can be demonstrated. However, the fact that such differences exist is not in itself sufficient evidence to warrant the conclusion that they are causal factors in distribution.

The experiment described below was designed to determine whether edaphic factors are likely to have a significant effect in the delimitation of two of the communities being studied.

The author is indebted to Mr. G. A. McIntyre, Division of Mathematical Statistics, C.S.I.R.O., for the statistical treatment of the data.

METHODS

Soil was collected from four locations within a Dry Sclerophyll Forest community in which the dominant species is *Eucalyptus rossii* Baker and Smith, and from four locations within a neighboring Savannah Woodland community in which the dominants are *E. melliodora* A. Cunn. and *E. blakelyi* Maiden. A description of the vegetation and soils, and of the method of sampling, has been given in a previous paper (Moore 1959). For the investigation described here, the soils of the two communities at Site 1, referred to in that paper, were used. The soils were sieved to remove stones and plant debris, and the four samples from each community thoroughly mixed before being placed in six-inch earthenware pots.

Seed of *E. rossii* and *E. melliodora* was sown on the surface of the soils on August 30, 1957, each species being sown both pure and mixed on each soil. When the seedlings were established, they were thinned to two uniform plants per pot. Water was added as required so that it was at no time limiting. There were twelve replications in a randomized block design.

The plants were harvested on February 7, 1958, 23 weeks after sowing the seed. Height and dry weight of the tops were recorded. (Drying 24 hours at 80°C.).

RESULTS

The results are shown in Tables I and II. When *E. rossii* and *E. melliodora* are grown in pure stands, there is no significant response to the soils on which these species grow, whether growth is measured as yield or as height. When grown in mixed stands, there is a clear differential response, each species in a relative sense growing best on its own soil. For mixed stands the interaction of species and soils is highly significant ($P < .001$ for both height and yield). On the *E. rossii* soils both yield per plant and height of *E. rossii* are greater in mixed than in pure stands ($P < .01$ for yield, $P < .05$ for height), while for *E. melliodora* the reverse holds ($P < .05$ for yield, $P < .001$ for height). The corresponding differences on the *E. melliodora* soils are not significant, but a similar pattern in reverse is evident.

TABLE I. Mean height per plant (cm.)

Species	Soil	Stand	
		Mixed	Pure
E. rossii	E. rossii	12.2	10.4
	E. melliodora	8.6	9.9
E. melliodora	E. rossii	7.7	11.6
	E. melliodora	10.0	10.7

TABLE II. Mean yield per plant (gm. d.m.)

Species	Soil	Stand	
		Mixed	Pure
E. rossii	E. rossii	1.53	0.96
	E. melliodora	0.74	0.96
E. melliodora	E. rossii	0.39	0.69
	E. melliodora	0.74	0.65

DISCUSSION

The results obtained in this experiment clearly indicate the possibility of an edaphic factor or factors influencing the distribution of the two species of *Eucalyptus,* and hence the delimitation of the communities in which they are the dominant species. The particular factors involved must be determined by additional experiments. It would no doubt be necessary to grow the plants for a longer period to measure the full effects, especially on the *E. melliodora* soil.

The implications of this work are of considerable importance in the study of plant communities in relation to habitat. Billings (1952) has pointed to the necessity of determining the tolerance limits of individual species before one can gain a complete understanding of community-habitat relationships, while Clapham (1956) and Major (1958) have emphasized the need for autecological studies of plants under conditions of competition with other plants.

The explanation of the effect of soil on vegetation is in part at least to be found in its effect on the relative vigor of the plants (Salisbury 1929). Tansley (1917) has shown that the absence of calcicoles on non-calcareous soils, and of calcifuges on calcareous soils, is in part due to the effect of the soil on the vigor of the plant, with consequent increase or decrease in its competitive ability. Gustafsson (1951) states that viability depends not only on the physical environment, but also on the community in which the species occurs. Ellenberg (1953, 1956, 1958) distinguishes between physiological tolerance (plants growing in monocultures) and ecological tolerance (plants competing with others), and concludes that relative competitive ability of a species varies with the environment, including competing species. Roussine (1957) has reviewed and summarized the work of a number of Russian biologists on the question of inter- and intraspecific relationships as presented by Sukachev (1953). It is pointed out that the plant community which develops on a given area is dependent not only on the physical environment, but also on the nature of the competitive effects, both inter- and intraspecific, of all the plants occupying the area.

The data presented here clearly indicate that the species reacts to the total environment, which includes competing species. The tolerance ranges of *E. rossii* and *E. melli-*

odora overlap in respect of some unknown edaphic factor. Thus, in pure stand, each species does equally well on the same soil, and both species show the same differential response when grown on the other soil. Either species, therefore, could become the dominant on either soil, provided it is not subjected to competition with the other species. But when the two species are grown in mixed stand, one species gains a clear advantage over the other at an early stage of growth. It would be anticipated that one would soon become the dominant, while the other would be suppressed, and probably subsequently elimnated.

In addition to studies of the factors of the environment and the tolerance limits of individual species, studies of the growth of plants in both pure and mixed stands under different conditions will be necessary to obtain a full understanding of plant-habitat relationships. Billings (1952) states that "Every plant species is distributed according to the tolerance ranges of its own ecotypes and biotypes. It is independent of other species except where individuals of other species constitute an integral part of its environment." The present study suggests that where the tolerance ranges of two species overlap, their distribution is not independent, but is determined in part by the presence or absence of the other during establishment. Jenny (1941, 1958), Major (1951) and Crocker (1952) have discussed in detail the dependent and independent aspects of the plant biotic factor, recognizing the floristic factor, or the flora, as one of the environmental factors determining soils and vegetation.

Gates *et al.* (1956) were able to demonstrate differences in the habitats of different communities in the salt deserts of Utah, but found no definite correlation between the habitat factors measured and the distribution of the communities. It is unlikely that chemical and physical analyses of the soils of a number of communities will in themselves provide an explanation of plant and community distribution. The reaction of the plants to different conditions must also be studied. However, the results reported by Gates *et al.* (1956) suggest the possibility of an overlapping of tolerance limits, and that a study of the growth of the different species in pure and mixed stands in soils obtained from the several communities might be expected to provide information relative to their distribution in the field.

SUMMARY

Two species of *Eucalyptus* (*E. rossii* and *E. melliodora*) were grown in both pure and mixed stands in soils obtained from neighboring communities in which the two species were the dominants.

The data indicate that the tolerance ranges for some edaphic factor overlap, and that under these conditions the presence or absence of interspecific competition will determine the community which develops on a particular site.

It is suggested that investigations of species distribution and plant-habitat relationships must include studies of interspecific competition in relation to habitat factors.

REFERENCES

Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. Quart. Rev. Biol. **27**: 251-265.

Clapham, A. R. 1956. Autecological studies and the "Biological Flora of the British Isles." Jour. Ecology **44**: 1-11.

Crocker, R. L. 1952. Soil genesis and the pedogenic factor. Quart. Rev. Biol. **27**: 139-168.

Ellenberg, H. 1953. Physiologisches und ökologisches Verhalten derselben Pflanzenarten. Ber. deutsch bot. Gesell. **65**: 350-361.

———. 1956. Aufgaben und Methoden der Vegetationskunde. Bd. IV, Teil I of H. Walter's "Einfuhrung in die Phytologie." Ulmer: Stuttgart.

———. 1958. Bodenreaktion (einschlie Blich Kalkfrage). Handbuch der Pflanzenphysiologie Vol. **IV**: 638-708.

Gates, D. H., L. A. Stoddart, and G. W. Cook. 1956. Soil as a factor influencing plant distribution on salt deserts in Utah. Ecol. Monographs **26**: 155-175.

Gustafsson, A. 1951. Some aspects of variation and evolution in plants. Evolution **5**: 181-184.

Jenny, H, 1941. "Factors of Soil Formation." McGraw-Hill: New York.

———. 1958. The plant factor in the pedogenic functions. Ecology **39**: 5-16.

Knapp, R. 1954. "Experimentalle Soziologie der höheren Pflanzen." Ulmer: Stuttgart.

Major, J. 1951. A functional, factorial approach to plant ecology. Ecology **32**: 392-412.

———. 1958. Plant ecology as a branch of botany. Ecology **39**: 352-363.

Moore, C. W. E. 1959. The nutrient status of the soils of some natural plant communities on the southern Tablelands of New South Wales. Ecology **40**: 337-349.

Roussine, N. 1957. Travaux phytosociologiques soviétiques des dernières années. Vegetatio **7**: 291-300.

Salisbury, E. J. 1929. The biological equipment of species in relation to competition. Jour. Ecology **17**: 197-222.

Sukachev, V. N. 1953. [On interspecific and intraspecific relations among plants.] Inst. Lesa. Soobshch, Akad. Nauk U.S.S.R. **1**: 5-44.

Tansley, A. G. 1917. On competition between *Galium saxatile* L. (*G. hercynicum* Weig.) and *Galium sylvestre* Poll. (*G. asperum* Schreb.) on different types of soil. Jour. Ecology **5**: 173-179.

C. W. E. MOORE

COMMONWEALTH SCIENTIFIC AND RESEARCH ORGANIZATION,
DIVISION OF PLANT INDUSTRY,
CANBERRA, A.C.T.

PALYNOLOGICAL STUDIES OF THE BARNSTABLE MARSH, CAPE COD, MASSACHUSETTS

At the annual meeting of the Ecological Society of America in Boston in December, 1953, Patrick Butler presented a paper under the above title. Owing to his accidental and untimely death in Alaska during the following summer Butler's study of the Barnstable Marsh was not completed, though he had already amassed a large body of data on the palynological and sedimentary history of this area of eastern Massachusetts. Fortunately he had prepared an abstract of the results obtained from analysis of the pollen and spores in one of the

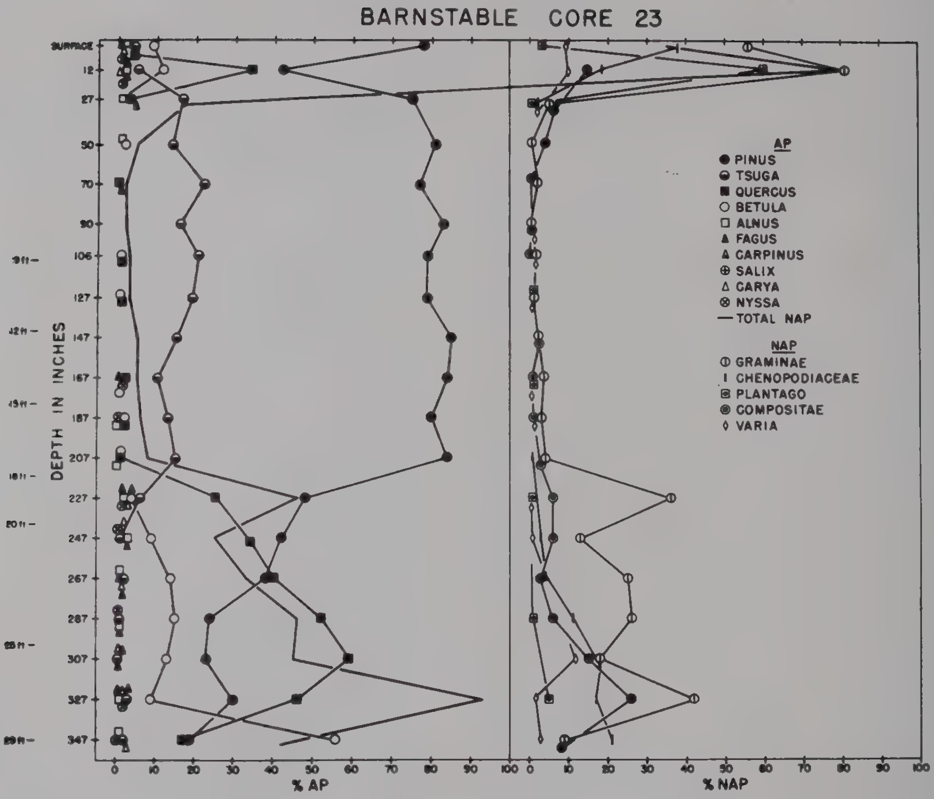


Fig. 1. Pollen diagrams from the Barnstable Marsh.

most significant and complete of his many cores. Discusion of his detailed study of this core (Barnstable core #23) comprised the substance of Butler's paper at the Boston meeting and the basis for his paleoecological interpretations of the vegetational history of the Barnstable Marsh. Subsequently A. C. Redfield relocated the site of this core, which was the deepest found in his transects of the marsh and extended approximately 347 in. from the surface, and secured samples of peat from four critical horizons. The samples were processed and the C^{14} activity measured by Meyer Rubin of the U. S. Geological Survey. Since the age determinations add significantly to the limited precise information available on the climate, vegetational change and rate of sea level changes during the past 5,000 years on the Massachusetts coast, Butler's abstract, pollen diagram, and the chronological data are presented herewith.

Abstract

(January 19, 1954)—The Woods Hole Oceanographic Institute has for the past two summers supported the field work of a study of the Great Marshes in Barnstable on Cape Cod. The purpose of the study is to find any changes in climate and sea level during the recent past in southeastern New England. It is hoped that this study will elucidate the age and developmental history of the marsh.

Last summer ten complete peat cores were taken at selected points across the widest part of the marsh. The pollen analysis of the deepest of these has been completed. The peat at this point is 29 feet deep.

The results (Figure 1) indicate that the marsh began to be formed at the end of the postglacial warm, moist period, which is usually said to have ended about 5,000 years ago. The warm, dry period which followed is reflected in the increase of oak, hickory and birch pollen. These genera dominate the pollen content of the peat from near the bottom of the core to about nineteen feet from the surface. Here, the pollen of these genera gradually give way to pine and hemlock. This indicates a return to cooler, more moist conditions which have lasted nearly to the present. A local increase in grass pollen and ash, hickory and birch near the top probably reflects the influence of white man on the vegetation over the past three hundred years.

Since the grasses forming the peat can grow only at rather restricted levels below mean high water, the implication is that there has been a gradual rise in sea level at least over the last 5,000 years. If the sea level has risen 29 feet in five thousand years, the average rate of rise along this part of the North Atlantic coast has therefore been about 6 or 7 in. per century.

Chronological Data and Conclusions

The site of Butler's core #23 was located at a point approximately 900 feet bearing 56° 50′ true from the intersection of U. S. Route 6 and the railroad, a short distance east of the West Barnstable Railroad Station. Table I gives the pertinent data on 4 samples of peat secured at this point. The peat samples were 2 in. in diameter and 6 in. in length and were taken from the indicated mean depth below the surface of the marsh, which in this area is a few in. above mean high water. The plant cover in the vicinity is dominated by *Spartina patens* (Ait.) Muhl.

TABLE I. Age and physical characteristics of Barnstable Marsh peat within increasing depth

Mean depth	C^{14} Age	USGS Lab. No.	Loss on drying	Loss on ingition	Ash	Character of peat
inches	yrs. BP		%	%	%	
21......	400± 100	W-677	72.6	6.3	21.2	fibrous
33......	770± 100	W-675	78.5	7.7	13.7	soft fibrous
207......	1880± 100	W-678	85.8	4.0	10.2	very soft fibrous
327......	5480± 120	W-676	54.1	4.7	41.2	firm fibrous

Although Butler's abstract presents only a bare minimum of his interpretation of the pollen profile, he added much detail to this in his oral presentation at the Boston meeting. Regrettably none of this exists in written form. Attention should be drawn, however, to several features of the pollen diagram which are of special interest, particularly in view of the currently established C^{14} dates.

The sample from 327 in., dated 5480 ± 100 yrs B.P. (Before Present), confirms Butler's estimate of the age of the lower portion of the core. His interpretation that this material, marked by a parallelism in the rise and fall in the percentage of oak and non-arboreal pollen, was produced at the end of the postglacial warm period is in close agreement with that of Johnson et al. (1942, 1949) made from studies of the Boylston Street Fish Weir in which evidence that the climate 5,000 years ago was somewhat warmer than at present, was drawn from a wide range of evidence.

The sample from 207 in., dated 1880 ± 100 yrs B.P., coincides with the horizon at which pine and hemlock became dominant, which Butler considered to indicate a return to cooler, moister conditions than at present. Because of the very soft character of the peat at this horizon coring was difficult and contamination of the sample by younger material may have caused the age to be undervalued.

The striking changes between 27 and 12 in. shown by the vast increase in non-arboreal pollen associated with increase in oak and decrease in pine seem assuredly to be assignable to European colonial influence in deforesting the New England coastal region, as Butler intimated. His inference is nicely supported by the radio-carbon date of 400 ± 100 years at the 21 ± 3 in. level. It should also be noted that the decline of non-arboreal pollen, increase in pine and decrease in oak between the 12 in. level and the surface conform consistently with phenomena which were induced by cultural changes in eastern New England during the middle and later 19th century, viz.: the abandonment of farms and the return of forest conditions over formerly cleared and cultivated areas. With exception of certain major urban centers this trend continues to the present.

The deepest highly organic sample, taken from 327 in. (approx. 27 feet), was immediately underlain by a deposit of compact pale blue-gray clay-like material exhibiting a loss on ignition of 2%. The thickness of this deposit is unknown. In gross physical character it is similar to the subsoil of nearby uplands. The sample at 327 in. appears to represent the earliest accumulation of a true peat at this position in the basin of the encroaching marsh and cannot have undergone appreciable vertical displacement as a result of compaction of the underlying sediments. In view of the fact that the entire peat column, from the present surface to the 327 in. level is comprised of salt marsh peat it is evident that a slowly progressing marine influence has been responsible for the aggradation of the entire body of the marsh peat. The age of the peat at the lowest level (approx. 5,500 years), therefore, indicates aggradation of a mean rate of 6 in. per century. This mean value almost precisely confirms Butler's estimate based largely on palynological considerations.

In connection with the complex problem of geologically recent sea level change on the New England coast this study of the Barnstable Marsh provides a very interesting and significant corollary to the postglacial sequence exposed in deep excavations in the city of Boston (Johnson et al., 1949). In the sedimentary complex exposed in the Back Bay area of Boston there is an estuarine sequence superimposed on a thin peaty horizon. The peat shows transition from fresh water forest swamps to salt marsh. The whole complex lies on the subaerially eroded surface of a late-glacial marine (?) clay. The stratigraphic sequence deduced from the paleobotanical evidence shows that the swamp forest was drowned by rising water, followed by development of a reed swamp (*Phragmites*) which in turn was suddenly terminated by a marine invasion followed by transitory thin salt marsh deposits (*Spartina*). The fresh water peat is at a depth of 25 ± 1 feet below the present mean tidal level (29 ± 1 feet below mean high water, and thus corresponding closely to the deepest Barnstable Core). The age of this peat, at the level immediately below the marine invasion, is 5,700 ± 750 years, indicating a mean rate of rise of sea level of a slightly less than 6 in. per century. This value is remarkably consistent with the evidence from the Barnstable Marsh, which lies about 60 miles to the southeast of the Boston basin. These values fall in line with radiocarbon measurements on peat and shell material from the coasts of Holland, Texas and Louisiana recently reviewed by Shepard and Suess (1956).

It should be emphasized that neither from the Barnstable Marsh studies nor from the Boylston Street Fish Weir data is it possible to distinguish whether submergence has resulted from crustal down warping or from eustatic rise of sea level.

REFERENCES

Johnson, F. et al. 1942. The Boylston Street Fish Weir. Papers of the Robert S. Peabody Foundation for Archaeology. Vol. 2.

Johnson, F. et al. 1949. The Boyston Street Fish Weir II. Papers of the Robert S. Peabody Foundation for Archaeology. Vol. 4, No. 1, p. 60.

Shepard, F. P. and Suess, H. E. 1956. Rate of post glacial rise of sea level. Science 123: 1082-1083.

PATRICK BUTLER[1]

---

[1] Formerly Graduate Student in the Faculty of Arts and Sciences, Department of Biology, Harvard University. This manuscript, prepared by Elso E. Barghoorn and Alfred C. Redfield, Harvard University, is contribution No. 1024 from the Woods Hole Oceanographic Institution.

PHOTOSYNTHESIS IN CONIFERS COMPUTED PER UNIT LEAF AREA, DRY WEIGHT, VOLUME, CHLOROPHYLL CONTENT AND RESPIRATORY RATE

Some years ago I published a table of photosynthetic rates under optimal near-natural conditions (Verduin, 1953). Rates were expressed per unit dry weight, area, volume, chlorophyll, and respiratory rate. At that time I did not find any reports of conifer photosynthesis which would permit computation of rates on these bases. The paper of Bourdeau (1959) brought the problem to my attention, and a little additional research made approximate computation possible. Bourdeau studied blue spruce, Norway spruce, Scotch pine and hemlock, and expressed his rates per gram fresh weight of stem or needles. He also reported the chlorophyll content and the moisture content. Because these trees are readily available in Bowling Green, I was able to collect specimens and measure the area and volume of needles per gram. For example, a 3 gram sample of blue spruce twig had 2.5 g of leaves, and contained 230 needles having an average length of 2.3 cm and a thickness of 1 mm. Thus average area per leaf was $2.3 \times 0.4 = 0.9$ cm^2, so the average leaf area per gram of leaf was 85 cm^2, and per gram of twig was 70 cm^2. The average volume per gram of leaf was 2 cm^3. The maximal net phtosynthetic rate reported by Bourdeau was 25 μg/g fresh twig/min. Respiration rate was 5, yielding a total of 30. This can be converted to $(30 \times 60)/70 = 26$ μg/cm^2/hr or 0.6 μmol/cm^2/hr. All the data necessary for computation of the other rate bases was provided in Bourdeau's paper. In Table I a comparison of spruce and apple is presented. Note that in every category spruce photosynthetic rates are distinctly below those of apple. Only in the ratio of photosynthesis to respiration does the spruce rate approach the apple rate, indicating that the low photosynthetic rate per unit of plant matter is matched by a proportionately low respiration rate. Apple was chosen for this comparison because a large volume of data are available confirming its high photosynthetic yield, which is similar to that observed in herbaceous plants (Verduin, 1953; Rabinowitch, 1951, p. 998-1001). It seems likely, however, that many other woody species exhibit such high rates. Moreover, the rates for the other conifers studied by Bourdeau are similar to those of spruce in Table I. I computed rates from Parker's (1953) work with *Picea excelsa* and found them also in close agreement with the data in Table I. If conifers are more efficient than deciduous trees in dry matter production, as Bourdeau states, then this characteristic is the more remarkable in view of the relatively low rates per unit of plant matter.

TABLE I. Comparison of spruce photosynthetic rate per unit area, volume, chlorophyll, and respiratory activity, with comparable rates for apple

Plant	MICROMOLES CARBON DIOXIDE ABSORBED PER HOUR				
	per mg dry wt	per cm^2 surface	per mm^3 volume	per μg chl	per μmol CO$_2$ respired
Spruce *Picea pungens*...	0.1	0.6	0.02	0.03	5
Apple *Pyrus malus*.....	1	4	0.2	0.1	9

REFERENCES

Bourdeau, P. F. 1959. Seasonal variations of the photosynthetic efficiency of evergreen conifers. Ecology **40**: 63-67.

Parker, J. 1953. Photosynthesis of *Picea excelsa* in winter. Ecology **34**: 605-609.

Rabinowitch, E. I. 1951. Photosynthesis II, 1. Interscience Publ. Inc. pp. 603-1208.

Verduin, J. 1953. A table of photosynthetic rates under optimal near-natural conditions. Amer. Jour. Bot. **40**: 675-679.

JACOB VERDUIN

BIOLOGY DEPARTMENT
BOWLING GREEN STATE UNIVERSITY
BOWLING GREEN, OHIO

THE SPREAD OF LEHMANN LOVEGRASS AS AFFECTED BY MESQUITE AND NATIVE PERENNIAL GRASSES[1]

INTRODUCTION

During the latter part of the 19th century, velvet mesquite (*Prosopis juliflora* (Swartz) DC, var. *velutina* (Woot.) Sarg.) began to spread out from the washes and alluvial flats onto open rangeland (Griffiths 1904). This spread has continued since that time until it has now become a major range management problem in southern Arizona, New Mexico and Texas. The mesquite's consumptive use of the limited water supply has been an important factor in all but eliminating native perennial grasses from extensive range areas (Parker and Martin 1952). In many instances ranges have deteriorated to such an extent that reseeding has become necessary. Several grass species have been investigated to discover those best suited for this use.

In the late 1930's, reseeding trials in New Mexico (Bridges 1941) indicated that Lehmann lovegrass (*Eragrostis lehmanniana* Nees.), native to the South African grassveld, established itself vigorously when seeded in many areas in the Lower Sonoran zone of the Southwest. It has proved to be most useful for reseeding depleted southwestern ranges in areas of 14 to 16 in. annual rainfall. A study conducted on the Santa Rita Experimental Range in southern Arizona (Parker and Martin 1952) showed that a heavy stand of mesquite lowered seedling establishment of seeded Lehmann lovegrass. Thinning the mesquite resulted in better seedling establishment. The study also showed that the competitive effect of mesquite on Lehmann lovegrass, though apparent, is much less marked than it is on native perennial grasses; and that forage production of the lovegrass increased as the number of trees decreased. The current

---

[1] Approved for publication as Tech. Paper No. 522, Arizona Agricultural Experiment Station.

study was made in an attempt to determine the effects of competition between mesquite, Lehmann lovegrass, and the native perennial grasses. Three phases were investigated: (1) The effect of mesquite on Lehmann lovegrass; (2) The effect of mesquite on native perennial grasses; (3) The result of competition between Lehmann lovegrass and native perennial grasses.

Description of the Study Area

Two areas on the Santa Rita Experimental Range were selected for study. In 1945 these areas (designated A and B) had been treated in the following manner. Four plots, each 202 feet by 404 feet (two acres) were thinned to mesquite densities of 0, 9, 16, and 25 trees per acre, while one two-acre plot was left with its original stand (358 trees per acre in area A, 138 trees per acre in area B) as a check. Only average size trees, at least 5 feet high with a minimum basal diameter of two in., were left, and these were evenly spaced. Along one edge of each plot a 50-foot-wide strip was seeded to Lehmann lovegrass by broadcasting and raking. Seedling establishment was satisfactory.

Area A, located in a foothill pasture at 4100 feet elevation has received an average of 15.6 in. of precipitation per year since the study was initiated. The soil borders between Coronado Stony Loam and White House Gravelly Loam. Being near water, it is subjected to heavy grazing yearlong. Area B, about two miles west of Area A, lies at an elevation of 3900 feet and has had an average annual precipitation of 14.2 in. during the same period. The soil is classified as Continental Sandy Loam. Area B is used as a holding pasture at shipping time and receives heavy grazing for a short time in the fall, but no use at other times. At the time the mesquites were thinned, native perennial grasses on both areas consisted principally of the following: Arizona cottongrass (*Trichachne californica* (Benth.) Chase), slender grama (*Bouteloua filiformis* (Fourn.) Griffiths), Rothrock grama (*B. rothrockii* Vasey), black grama (*B. eriopoda* Torr.), sideoats gramma (*B. curtipendula* (Michx.) Torr.), sprucetop grama (*B. chondrosioides* (H.B.K.) Benth.), plains bristlegrass (*Setaria macrostachya* H.B.K.), and perennial threeawns (*Aristida* spp.). The density of grasses on area A was roughly three times that on area B.

Collection of Data

In the fall of 1958 each area was divided into 5 two-acre plots; i.e., one plot in "A" and one plot in "B" for each of the 5 mesquite densities. The perennial grass cover on the two areas was sampled using the following method: Six line transects 30 feet apart and running the full length of the plot were located in each plot. In area A, 12 stations were located along each line at 35-foot intervals. The first station was located 35 feet from the base line of the plot. In this manner 72 stations were located within each plot. In area B, because of a lower grass density, the stations were located only 30 feet apart, giving a total of 84 stations in each plot. This measurement technique not only made it possible to correlate mesquite density with number of grass plants; it also permitted obtaining a record of spread of the lovegrass from the original seeding. The perennial grass cover was recorded at each station with the use of a 0.1 square meter quadrat frame. The frame was dropped at each station, and all the perennial grasses within the frame were counted. Grasses were recorded in two categories: (1) Lehmann lovegrass and (2) all native perennial grasses.

Effect of Mesquite on Grass Densities

The treated plots had more Lehmann lovegrass than the check plots in both areas. In area A, Lehmann lovegrass density per square meter was 7.8 plants in the check plot, and ranged between 10 and 12.5 plants in the treated plots. In area B, a less productive site, Lehmann lovegrass density per square meter was 1.3 plants in the check plot, and averaged from 5 to 6.8 plants in the treated plots. None of the plots in either area where mesquite had been thinned or removed showed a statistically significant variation in the amount of Lehmann lovegrass established under any degree of thinning.

Density of the native grasses was affected adversely by even a few mesquite trees (Fig. 1). In the check plots, where mesquite trees were numerous, perennial native grass density was low, about 10 plants per square meter in area A and 6.5 plants per square meter in area B (Fig. 2). Where the mesquite stand was reduced to 25 trees per acre, the native grass density increased to 17.5 plants per square meter in area A and 8.5 plants in area B; an increase of 75% and 25% respectively. The plots from which all trees had been removed showed a further increase in the number of native grasses (Fig. 3). Area A had about 35 plants per square meter and area B 14 plants. Native grass density was 100% greater on area A and 60% on area B than where the trees had been thinned to 25 per acre.

Although these density measurements refer only to number of plants per unit area rather than volume production, a previous study (Parker and Martin 1952), in which herbage yields were calculated from clippings, indicated a similar increase in herbage production as a result of mesquite thinning. The increase in number of native

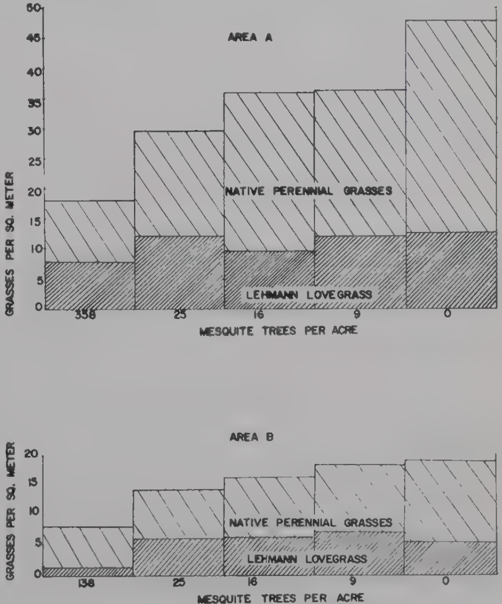


Fig. 1. Density of mesquite trees per acre in relation to density of native grasses per square meter.

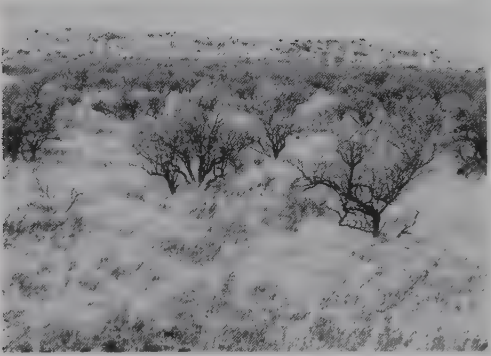


Fig. 2. Area A, check plot; mesquite density of 358 trees per acre; grass composition is Lehmann lovegrass and native perennial grasses.

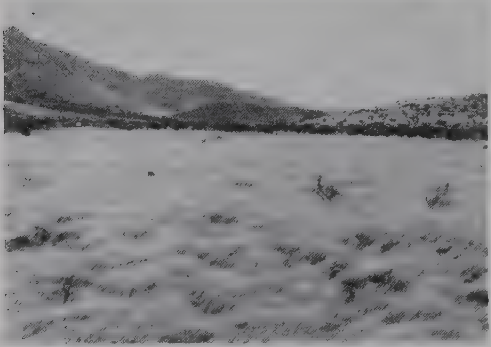


Fig. 3. Area A, treated by removal of mesquite in 1945, shows a grass density almost three times that of the untreated plot shown in Figure 2.

grasses that has been noted here might well have been even more marked had it not been for the Lehmann lovegrass competition.

Interaction Between Lehmann Lovegrass and Native Perennial Grasses

The grasses recorded in a row of quadrats at a given distance from the seeded strip constituted a sample of the grass density at that distance. For example, in area A, in the plot with zero trees per acre, the grasses in all quadrats 35 feet from the base-line were considered as one sample. The grasses in the quadrats 70 feet from the base-line were considered similarly, and so on. In this manner densities of Lehmann lovegrass and native perennial grasses were recorded in each plot at increasing distances from the strip that had been seeded to Lehmann lovegrass (Figs. 4 and 5).

Although the grass density was lower in area B than in area A the general Lehmann lovegrass migration pattern was the same in the two areas. In number of lovegrass plants, no statistically significant difference among the treated plots was found in either area. However, there was an inverse relationship between native grass density and rate of invasion of the lovegrass. Where native grass density was high, Lehmann lovegrass did not invade as far as it did where native grass density was low. Thus, Lehmann lovegrass extended 100 to 200 feet farther into the plots that had a low native grass density.

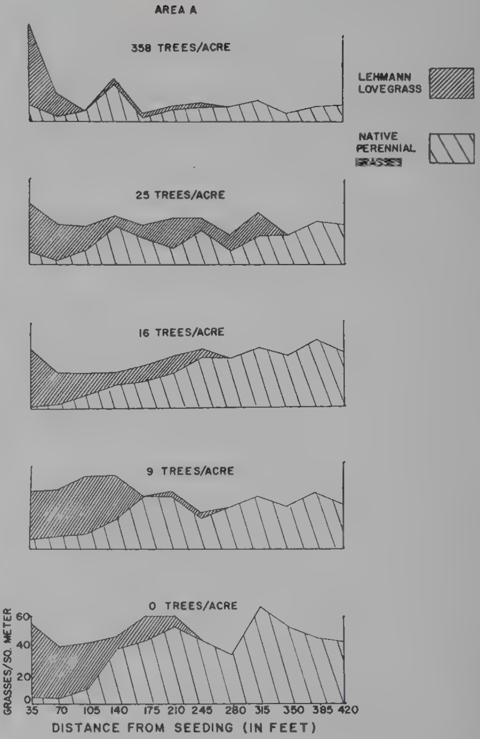


Fig. 4. Interaction in Area A between Lehmann lovegrass and perennial grasses at various densities of mesquite trees (see text).

The native grasses were not disturbed when the Lehmann lovegrass was seeded. In view of this, the density of native grasses should have been essentially uniform across the entire plot had there been no competition from Lehmann lovegrass. However, this competition appears to be the factor that has reduced the density of the native grasses. In areas invaded by Lehmann lovegrass, the total perennial grass density was generally no higher than in areas containing only native grasses. The relationship was such that in some samples a high lovegrass density was accompanied by a low native grass density, and in other, sometimes adjacent samples, the reverse was often the case.

Discussion

The establishment and spread of Lehmann lovegrass on the study areas, even where mesquite densities were as high as 25 trees per acre, indicates that this grass is able to become established and to perpetuate itself under the prevailing climate-soil complex with less than the precipitation that has fallen during the 13-year period since the areas were cleared and seeded. Maximum annual precipitation on area A during the period was 25.2 inches in 1958; minimum was 8.1 inches in 1956; mean annual was 15.6 inches. On area B, maximum annual was 18.9 in 1958; minimum was 9.3 in 1953; mean annual was 14.2. These figures do not tell the full precipitation-

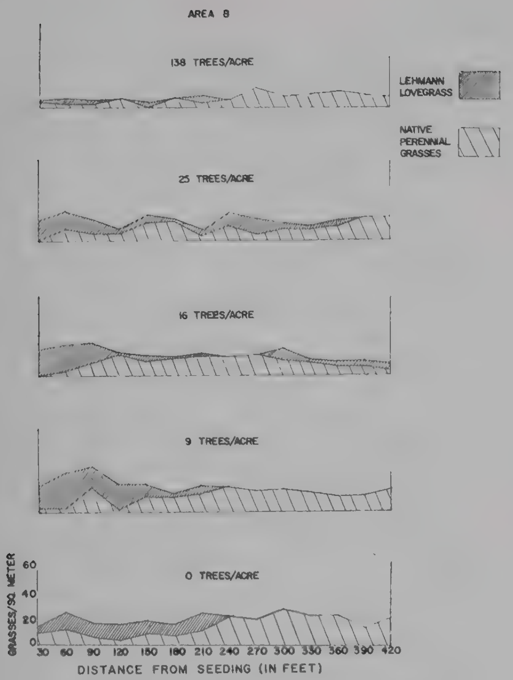


Fig. 5. Interaction in Area B between Lehmann lovegrass and native perennial grasses at various densities of mesquite trees.

effectiveness story; they do indicate something as to prevailing moisture conditions. Mesquite is a heavy user of water (McGinnies and Arnold 1939), yet despite this, the lovegrass has not only become established, but it has successfully moved out into adjacent areas. It would appear from this study that in some, and perhaps most, areas with dense stands of mesquite, the trees need not be completely eradicated but must be thinned if seedings of Lehmann lovegrass are to be successful.

As Lehmann lovegrass migrated into the area, it replaced rather than supplemented the native grasses. In regions of low rainfall, there is enough soil moisture to support only a limited total grass density of all species. Those species best able to compete and to survive during severe drought persist while those less hardy die out. In view of the increasing relative abundance of Lehmann lovegrass when competing with native grasses, it appears that the lovegrass occupies a superior competitive role.

Lehmann lovegrass occurs early in plant succession in its native habitat (Chippendall *et al.* 1955). This characteristic has made it extremely useful in reseeding depleted ranges in the southwestern United States. Once established in the Southwest, however, on ranges that support native grasses, it appears to compete with the native species on a more than equal footing (Humphrey 1958). Its advance is retarded somewhat but not prevented, by competition from a vigorous, well-established stand of native grasses. Where the native grass is sparse, Lehmann lovegrass spreads more readily.

The philosophy that reseeding is seldom justified on ranges having a fair remnant of native perennial grasses is emphasized in range reseeding recommendations of the Arizona Agricultural Experimental Station (Anderson *et al.* 1957).

The results of this study lend specific support to the more general recommendations of the Experiment Station, by indicating that reseeding Lehmann lovegrass on areas cleared of mesquite may not be advisable when adequate remnants of native perennial grasses are present. Forage production from the relatively more palatable native grasses is generally equal to or higher than that of a combined native grass-Lehmann lovegrass stand. Although removal of mesquite releases the native grasses, seeding Lehmann lovegrass serves only to reintroduce competition from another source. Admittedly less palatable to cattle, Lehmann lovegrass is grazed less heavily than are most native grasses. As Lehmann lovegrass progresses into an area, the native grasses tend to die out, apparently as a result of competition and selective grazing.

SUMMARY

In 1945, the mesquites on a series of two-acre plots on the Santa Rita Experimental Range were thinned to densities of 0, 9, 16, and 25 trees per acre. A fifth plot was left with its original heavy stand. A 50-foot-wide strip along one edge of each plot was seeded to Lehmann lovegrass. This study was conducted to discover the effects of competition between mesquite, Lehmann lovegrass and native perennial grasses. Conclusions reached were: (1) Mesquite densities of 25 trees per acre or less do not significantly reduce Lehmann lovegrass establishment. (2) Native grass density is affected adversely by even a few mesquite trees. Native grass density increased up to 75% where mesquite had been reduced from a dense stand to 25 trees per acre, and was approximately twice as great in the plot with no mesquite as in the plot with 25 trees per acre. (3) Although removal of mesquite released the native grasses, seeding Lehmann lovegrass served only to reintroduce competition from another source. As the lovegrass spread from the seeded strip into the area, it reduced and eventually largely replaced the native grasses. In places where Lehmann lovegrass had not invaded, the density of native grass was generally equal to or higher than that of combined native grass-Lehmann lovegrass stands. Reseeding an area cleared of mesquite thus appears to be of little or no value if remnants of native perennial grasses are present.

REFERENCES

Anderson, D., L. P. Hamilton, H. G. Reynolds and R. R. Humphrey. 1957. Reseeding desert grassland ranges in southern Arizona. Arizona Agr. Expt. Sta. Bul. **249**. rev. 31 pp. illus.

Bridges, J. O. 1941. Reseeding trials on arid range land. New Mexico Agr. Expt. Sta. Bul. **278**. 48 pp. illus.

Chippendall, Lucy K. A., J. D. Scott, J. J. Theron, D. Meredith and others. 1955. The grasses and pastures of South Africa. Central News Agency, Johannesburg, Union of South Africa. 771 pp. illus.

Griffiths, David. 1904. Range investigations in Arizona. U. S. D. A. Bur. Plant Industry Bul. **67**. 62 pp. illus.

Humphrey, R. R. 1958. Lehmann's lovegrass, pros and cons. Arizona Cattlelog **13**: 16-18.

Kearney, T. H. and R. H. Peebles. 1951. Arizona Flora. University of California Press. 1032 pp. illus.

McGinnies, W. G. and J. F. Arnold. 1939. Relative water requirements of Arizona range plants. Ariz. Agr. Expt. Sta. Bul. **80:** 167-246. illus.

Parker, K. W. and S. C. Martin. 1952. The mesquite problem on southern Arizona ranges. U. S. D. A. Circ. 908. Southwestern Forest and Range Expt. Sta. 70 pp. illus.

D. R. KINCAID, G. A. HOLT, P. D. DALTON
AND J. S. TIXIER[2]

---

[2] Graduate students in Watershed Management, University of Arizona, Tucson, Arizona. The authors gratefully acknowledge the assistance given by Dr. R. R. Humphrey, Professor of Range Management, in setting up this study and in reviewing the manuscript.

PLANT POPULATIONS IN BLUEBERRY STANDS DEVELOPED FROM ABANDONED HAYFIELDS AND WOODLOTS[1]

INTRODUCTION

When buying additional blueberry land, growers prefer abandoned hayfields rather than areas that have recently been cleared of forest trees. Undoubtedly, abandoned farmland is easier to manage and many growers believe that the former hayfields support fewer plants that are serious competitors of the blueberries. Since the vegetation of the two types of areas has not been previously compared, representative stands of each of the two types were selected and their plant population studied.

MATERIALS AND METHODS

The fields for this investigation are located on the Blueberry Experimental Substation, operated by the Canada Department of Agriculture, at Tower Hill, Charlotte County, New Brunswick. Information on the age of the fields was supplied by Mr. E. L. Eaton, Chairman of the Research Committee of the Tower Hill Blueberry Substation. The practices used in blueberry culture, the geographical area, the soil, and the weather of the area are described in a previous paper (Hall 1955).

Three stages in succession were selected: group 1, 5 blueberry fields that have been in production 10 years and were developed from abandoned hayfields which were last plowed about 25 years ago; group 2, 5 blueberry fields that have also been in production 10 years and were developed from woodlots which were cleared of trees about 25 years ago; and group 3, 5 blueberry fields that have been in production 25 years and were developed from two hayfields and three woodlots. In group 3, the former hayfields were last plowed 40 years ago and the former woodlots were cleared of trees at approximately the same time.

During the last two weeks of June 1957, species counts were made in all these fields by recording the plants occurring at one yard intervals on a 100-yard line transect, selected at random. Bare ground was recorded as a unit if no species occurred at any given yard-interval point on the transect.

RESULTS AND DISCUSSION

The frequency of occurrence of the species below the yard interval points of the line transects is summarized in Table I for each of the 3 groups.

TABLE I. Frequency of occurrence of species in 15 blueberry stands developed from abandoned hayfields and woodlots at Tower Hill, Charlotte County, New Brunswick

Species	Fields recently developed from abandoned hayfields	Fields recently developed from woodlots	FIELDS FORMERLY DEVELOPED FROM	
			abandoned hayfields	woodlots
Bare ground	19	36		45
Polytrichum commune	23		3	
Dennstaedtia punctilobula*		27		2
Pteridium aquilinum		15		
Danthonia spicata	10	4	5	2
Agrostis tenuis	106	2	25	
Luzula multiflora	9			
Populus tremuloides		2	17	8
Betula populifolia		5		3
Spiraea latifolia	56	29	50	15
Pyrus melanocarpa	2	9	5	16
Prunus pensylvanica	1	16		
Trifolium repens	11			
Epilobium angustifolium		3		5
Cornus canadensis		39		37
Rhododendron canadense		15		2
Kalmia angustifolia	2	22	40	68
Vaccinium myrtilloides	19	131	40	56
V. angustifolium var. laevifolium	107	114	230	210
V. angustifolium var. nigrum	3	8	62	25
Solidago rugosa	21	3		
Aster lateriflorus	8	3		
Hieracium pilosella	7			
Hieracium aurantiacum	14			
Hieracium pratense	37	4	8	
Others (less than 5 each)	45	13	15	6
	500	500	500**	500**

* Scientific nomenclature of vascular plants follows Gray's Manual of Botany, 8th ed., by M. L. Fernald.

** Columns 1 and 2 are based on 500 determinations (100 per field), column 3 on 200, and column 4 on 300. The figures of columns 3 and 4 have been adjusted for comparison.

Dennstaedtia punctilobula, Pteridium aquilinum, Populus tremuloides, Betula populifolia, Cornus canadensis and *Rhododendron canadense* occurred in fields recently developed from woodlots (Table I). All these are predominantly woodland species and are considered as weeds by Trevett (1952). These plants have probably survived from the previous woodland rather than arising from introduced seed.

The weeds *Pyrus melanocarpa, Prunus pensylvanica* and *Kalmia angustifolia* occurred in both types of new stands, but were more numerous in fields developed from woodlands. This is significant, because *Kalmia angustifolia* is one of the worst weeds in blueberry fields. The stronger rhizome, root, and shoot growth of this weed suppresses the growth of the blueberry plants. On the fields in production for a long time a marked increase of this same weed was also noted, indicating that continued control measures are necessary. Otherwise the population of this weed tends to increase until blueberry growing becomes unprofitable.

---

[1] Contribution No. 1759 from the Botany and Plant Pathology Division, Science Service, Canada Department of Agriculture, Ottawa, Ontario.

The six species occurring with the highest frequency in the blueberry fields developed from abandoned hayfields were: *Polytrichum commune, Agrostis tenuis, Spiraea latifolia, Solidago rugosa* and *Hieracium pratense*. The only serious weed among these was the shrub *Spiraea latifolia*.

The frequency of occurrence of species and varieties of blueberries, genus Vaccinium, was different in the various stages of succession; *V. myrtilloides* occurred most frequently in blueberry stands recently developed from woodlots. The lower frequency of occurrence of *V. myrtilloides* in older stands indicates that cultural practices, probably burning, were unfavorable to this species. This is in agreement with Camp (1945) who stated that this species declined with burning and was tolerant of shade, often persisting in second growth forests. In the stands of blueberries recently developed from abandoned hayfields *V. angustifolium* var. *laevifolium* was the most prevalent. This variety, which is the preferred blueberry, was the most prevalent species in the older stands regardless of origin. Individual clones, however, may react quite differently than the taxon as a whole; for example, a high-yielding clone which spreads very slowly may be dominated by a low-yielding clone with strong vegetative growth. In older stands the increase of *V. angustifolium* var. *nigrum* was more marked than that of var. *laevifolium*. The composition of these stands is rapidly changing and will undoubtedly be quite different after a period of 10 or more years.

SUMMARY

At Tower Hill, Charlotte County, New Brunswick, many of the plant species present in woodlots tended to persist in land cleared for native blueberry production and to present serious weed problems. In contrast to the stands developed on former woodlots, blueberry stands developed on abandoned hayfields had fewer weeds, and the weeds that did occur were present in lower proportions.

Vaccinium myrtilloides is a species inhabiting second-growth forests of the area and its frequency of occurrence in commercial fields decreased under the system of burning used in blueberry culture. *V. angustifolium* var. *laevifolium* was more characteristic of the abandoned hayfields, and the frequency of occurrence of this taxon and of *V. angustifolium* var. *nigrum* increased under the same cultural conditions.

REFERENCES

Camp, W. H. 1945. The North American blueberries with notes on other groups of Vacciniaceae. Brittonia **5**: 203-275.

Hall, I. V. 1955. Floristic changes following the cutting and burning of a woodlot for blueberry production. Can. J. Agr. Sci. **35**: 143-152.

Trevett, M. F. 1952. Control of woody weeds in lowbush blueberry fields. Maine Agr. Exp. Sta. Bull. **499**: 1-23.

IVAN V. HALL

PLANT PATHOLOGY LABORATORY,
KENTVILLE, NOVA SCOTIA, CANADA

Treatise on Marine Ecology

In 1940 the late Dr. T. Wayland Vaughan organized a subcommittee on the ecology of marine organisms in the Division of Geology and Geography of the National Academy of Sciences. Two years later the subcommittee was elevated to a full commitee with the title "Committee on Marine Ecology as Related to Paleontology." A series of progress reports was issued annually, and eventually a two volume treatise was published by the Geological Society of America. The present review is concerned with the first volume,[1] devoted to the science of marine ecology, especially as it relates to paleoecology which is the subject of volume two.

Volume one of this gigantic memoir contains 29 chapters, embracing the entire scope of marine ecology—physical, chemical, and biological. Chemical and biological oceanography are better and more fully represented than physical oceanography. By coincidence the number of authors also totals 29, but the relationship is not the obvious one of one chapter per author. The editor prepared six chapters, and several chapters were written by multiple authors. Roughly one-third of the writers are or have been on the staff of the Scripps Institution of Oceanography, one-third are from other American institutions, and one-third are European oceanographers. In addition to the text chapters, there are 36 annotated bibliographies prepared for the most part by taxonomists who have reviewed the ecological literature concerned with their taxonomic specialty.

The 29 text chapters are concerned with such topics as physical and chemical environments in the sea; the interaction and distribution of marine organisms; descriptions of plankton, estuaries, bottom communities, intertidal communities, coral reefs, the deep sea in general, and specific descriptions of the Baltic Sea, the Black Sea, and the Caspian Sea. Special chapters are also devoted to lunar periodicity, fluctuations in littoral populations, and mass mortality in the sea. The annotated bibliographies range through all of the major taxonomic groups from bacteria to mammals which are found living in the sea. Some of the larger groups such as Protozoa, Mollusca, Crustacea, and Echinodermata are subdivided and treated by several specialists. With few exceptions, the authors of the text chapters and annotated bibliographies are the leading students in their respective fields. In general the volume reviews present knowledge of marine ecology and, more specifically, relates this body of knowledge to the ecological interpretation of paleontology. Both goals are successfully attained, although the latter one is quite variable from chapter to chapter.

The scope of this volume and the mass of data and interpretation presented are so great that no one person could have prepared it alone. Likewise, it is impossible for a single reviewer to comment competently on all phases covered in this monograph. In spite of the gigantic size of the volume, it was still necessary for each author to select that material which seemed most suitable for his purpose; and obviously neither the text nor the bibliographies could be complete. The references which are given would undoubtedly lead one to the bulk of the world's literature in marine ecology. Some of the annotations are appraisals of the work rather than a digest or abstract of the paper.

With such a large number of contributors, one could not expect uniformity of treatment or of style of writing. Since most of the illustrations were borrowed from diverse sources, variations are naturally expected; some of them are highly polished and some of them are crude. A few of them were reduced too much, and in several cases they are hardly legible without the aid of a magnifying glass.

Specialists will, of course, find details about which they disagree or in some cases will prefer a different interpretation. This reviewer, for example, noted certain matters about which he would raise questions. The early history of the Marine Biological Laboratory at Woods Hole, Massachusetts, gives a misplaced emphasis to the role of Louis Agassiz, which was initiated by Lillie's history of that institution. Dr. Hedgpeth traces the idea of a flow of energy through a food cycle only as far back as the 1942 paper of Lindeman. Actually this rather simple and basic idea goes far back in the thinking and concepts of ecologists who have been concerned with studies on food chains and food cycles. In a review of methods of sampling marine organisms, Dr. Hedgpeth concludes that the Petersen bottom sampler is the best instrument. He fails to point out, however, that there are many situations (for example, rocks and hard sand) where this type of sampler is useless. In some such situations methods criticized in the review are much more effective in those special conditions for which they were devised than is the Petersen sampler.

The explanation of monosexual populations of *Craspedacusta sowerbii* is attributed to Russell (p. 898), but actually this was first proposed by Fernandus Payne and was repeated by Russell. Lake Baikal is given as an example by L. A. Zenkevitch of a body of water far removed from the Caspian Sea which is inhabited by the freshwater polychaete *Manayunkia* (p. 900), but Lake Erie which is a better example is not mentioned. Gunnar Thorson makes the statement that "Fishes are the highest link in the food chain" (p. 500), apparently neglecting the fact that turtles and seals feed on the fishes even if one wishes to disregard the marine birds. In discussing the scarcity of vertebrate bones at the bottom of the ocean, Margaretha Brongersma-Sanders does not consider as a possibility chemical solution of the bones, which has recently been suggested by studies at Fordham University.

In a monograph devoted to the principles of marine ecology and paleoecology, it was surprising to find a problem of natural resource conservation (p. 909) discussed in one chapter. As a problem in fisheries' management, it is most interesting and instructive but rather unexpected and not likely to reach many of those interested in practical problems of management. Some of the chapters were completed up to five years before publication, and hence do not include recent advances. For example, the chapter on lunar periodicity was completed before publication of the thought-provoking paper by LaMont Cole on the matter of periodicity, which is not considered in this volume. Dr. Hedgpeth failed to realize (p. 45) that some successions of marine communities described by this reviewer were physiographic successions rather than biotic successions, and that those communities were in areas on the verge of being cut off from the ocean rather than typical oceanic habitats. The use of the expression "adult community" by Dr. Thorson (p. 471) rather than the more common expression "climax community" seems to be unnecessary. In the chapter on "Interrelations of Organisms" it is surprising that predation is not considered. The range of *Limulus* is not given accurately in the chapter by Gordon Gunter (p. 173). Actually *L. polyphemus* extends far northward beyond Cape Cod as a common animal.

---

[1] Hedgpeth, Joel W. (editor). 1957. Treatise on marine ecology and paleoecology, Vol. I. Ecology. (Symposium) Geological Society of America, Memoir 67, prepared under the direction of a committee of the Division of Earth Sciences, National Research Council, National Academy of Sciences. Waverly Press, Baltimore. viii + 1296 pp. 4 portraits, 6 folding maps, 297 figures. $12.50.

Typographical errors are not unduly numerous considering the magnitude of this volume, and every writer knows the difficulty of producing published work without such errors. Most of those noted in this work are of little importance, but a few are regrettable. For example, the names of three authors are misspelled in the Table of Contents, and the death of Karl P. Schmidt is reported (p. 1213) as occurring four years before it actually occurred. There are a number of minor typographic errors, and some instances where taxonomic names are incorrect. The eel is referred to as an anadromous fish rather than as a catadromous species (p. 795). Such errors are rarely of consequence, but it is unfortunate that a number of errors appear in the bibliographies which may very well be copied and hence perpetuated for years to come. For example, the authors of the Allee, Emerson, Park, Park, and Schmidt text are out of proper sequence (p. 12); a paper by Pearse, *et al.*, is attributed to Oliver, *et al.* (p. 606).

Every marine biologist and ecologist will find much of great value in this volume. Each specialist will find here a convenient review of those phases of marine ecology outside of his own specialty. The book is more than a compilation—it is a critical study, well organized, and expertly prepared. Points of disputation by others will only serve to advance the development of marine ecology. This is a coöperative venture of giant proportions in which many of the most eminent marine ecologists have contributed. The complexity of ecology is frequently pointed out in the discussions, which is a most desirable feature and a much needed emphasis for the beginning student. In addition to setting forth the ecological principles for the interpretation of paleoecology, this volume will also serve as a standard source book in the pure science of marine ecology.

RALPH W. DEXTER

DEPARTMENT OF BIOLOGY
KENT STATE UNIVERSITY
KENT, OHIO

A MARINE BIOLOGY SYMPOSIUM

In the spring of 1956, scientists of many kinds were brought together at Scripps Institute of Oceanography to help create perspective as to the best directions to be followed in further research in marine biology. By implication the results of the symposium were to be used to help Scripps Institution plan the spending of a million dollar grant from the Rockefeller Foundation.

By design part of the group were aquatic scientists whose work concerned populations, processes, and patterns of life in the sea; the other part of the group included scientists whose work was related to the aquatic environment only because they were working with general aspects of living systems. A very strange combination of distinguished men thus met in discussion and in sessions at which invited papers were presented emphasizing approaches. The papers are the subject of a new book.[1]

In its organization the book, like the conference plan, is bizarre. In part 1 are 13 papers on ecology; in part 2 are 10 papers on biochemistry and physiology plus two of the best ecological papers on environmental productivity strangely misclassified as physiology (Margalef and Rodhe); in part 3 are 4 papers classified as behavior; and in part 4 are 12 papers classified as genetics and evolution.

Although all papers emphasize approaches, the papers do not present approaches in the same way. Some are new research results given as examples; some are reviews; some are viewpoint statements; and some contain suggestions for further research. Selected and valuable comments are published after each paper. The volume is thus an assortment of mixed orientation and subject with notions, opinions, misgivings, half-baked hunches, and statements of hope. The book is a showcase at which many of the participants were presenting a sample of their best. Marine genetics is heavily emphasized for a subject in its infancy.

Permeating the book is a semantic argument which developed around the word "experiment." Early in the conference A. C. Redfield shocked some of his associates by setting up an antithesis between environmental science and experiment. The argument degenerated into a conflict between indoor and outdoor science. The editor added further confusion by misrepresenting environmental science as only descriptive.

For purposes of this review papers are grouped into 5 systems of approach. All are at least partially experimental in conceptual basis. It is abundantly clear that all of the five approaches are good, with underdeveloped potential.

Approach 1: Study of Marine Organisms for Their Inherent Interest

In this approach are included neither those who use the animals as means for understanding ecological systems nor those who use the animals as a tool for understanding general living systems. Among these studies may be Kon's study of the comparative distribution of vitamins in marine organisms; W. L. Belser's brief comment on the studies needed on marine micro-organisms; V. Loosanoff's interesting accounts of unsolved problems with shellfish; D. L. Ray's listing of some invertebrates which have interesting habits that fit them for experimental studies; W. Wieser's account of super-numerosity of related species of microfauna in the benthos; Y. Matsui's account of the pearl oyster *Pinctada*, its physiology, and pearl chemistry; R. Lewin's account of complex reproductive life cycles in the marine algae; Barigozzi's account of genetics in some aquatic species; and Montalenti's discussion of sex-ratio phenomena in the population genetics of some marine species.

---

[1] Buzzati-Traverso, A. A. (editor). 1958. Perspectives in marine biology. A symposium held at Scripps Institution of Oceanography, University of California, March 24-April 2, 1956. University of California Press, Berkeley and Los Angeles. xvi + 621 pp., figs. & tables. $10.00.

Approach 2: Laboratory Studies on Marine Species Followed by Comparative Interpretation of Their Behavior and Functions in the Environment for the Purpose of Understanding Large Scale Phenomena in Nature

D. M. Rae advocated the development of a plankton husbandry, pointing to the negligible progress in culturing planktonic zooplankton and the shadowy suspicions of influence of organic compounds in water masses. C. M. Yonge described experiments with corals and other animals which have symbiotic zooxanthellae and attempted to interpret the workings of reefs from data of the laboratory.

Luigi Provasoli's discussion of vitamin requirements of marine algae in the laboratory and vitamin distribution in nature involved joint use of the field observational and autecological methods. P. Miyadi used indoor facilities to interpret large scale outdoor phenomena involving marine fish behavior. A. Hasler reported experiments with fishes involving migratory responses and evidences from observations of migratory movements in nature. T. Waterman compared the patterns of polarized light in the sea and the responses of some marine animals in experimental studies with polarized light in the laboratory.

Approach 3: Intensive Observational and Analytic Study of Bottom Animals in the Environment

On the side of approaches of environmentally oriented science was a brief statement (in absentia) by the Russian Zenkevitch pointing out the advantages of wise international cooperation in ocean-wide sampling studies. Pierre Drach of the University of Paris recommended qualitative and quantitative description of the sea bottom faunas. Riedl urged better bottom sampling equipment. Thorson and Douglas Wilson reviewed papers on bottom animals and larval stages discussing the presence of parallel species in different areas with similar roles and the prevalence of physiological mechanisms in animals which permit species to complete life cycles by larval settlement on a bottom environment of suitable type. W. Wieser presents data on the distribution of deposit feeders in which both comparative functional anatomy and comparison of bottom types are involved. Barnes presents results of photography of bottom animals and plankton with underwater television.

Approach 4: Study of Environmental Processes in the Field with Modern Techniques and Experimental Concepts

Rodhe, Vollenweider and Nauwerck presented the results of extensive radioactive carbon studies of photosynthesis in lakes with implications drawn about methods, chlorophyll, and seasonal and vertical patterns of natural photosynthesis. Margalef's paper on the species patterns in natural systems and its comparison to entropy functions is a major contribution in experimental thinking with observational data in giant systems. The successful correlation of causative factors and biological events is reported by A. C. Hardy in the waters about England. This is an example of the use of natural experimental situations of the great sea systems. Selected samplings of natural test situations are provided by Tonolli for plankton distribution in space and by Bogorov for seasonal distributions.

Approach 5: General Study of Living Processes

A number of the participants advocated study of the general problems of living systems without special reference to the sea or to marine animals as the quickest approach. C. S. Pittendrigh reported on biological clocks in *Drosophila* and *Euglena*. F. Brown summarized his evidences of endogenous cycles related to external cycles. A Szent-Györgi presented his latest theory of muscle function. E. S. Guzmann Barron reported some miscellaneous kinds of cellular experiments done at a marine station. T. Bullock discussed the fluid state of knowledge and the lack of unifying principles in the physiology of adaptation and homeostasis. Novick summarized the microbial evolution which could be observed in biochemical adaptation in a chemostat. Thorpe discussed mechanisms and descriptive terms concerning behavior. D. I. Arnon presented an account rich with examples concerning the role of micronutrients in plants.

Few are likely to find objection to these reports of well-known scientific approaches, but there are likely to be many who ask what these reports have to do with the sea. Marine phenomena involve basic living processes but are also larger, different, and born of a composition of physical cycles, ecosystems and populations of organisms.

It cannot be said that perspective in marine science was created by the 8 page summarizing section. Buzzati-Traverso confuses his classification separating "biological studies" from "oceanographic studies" by a scramble of ecological topics in both. Many study organisms only so as to understand the sea; others study the sea only for its organisms.

Much better perspective can be found in the published comment of one participant, Bostwick Ketchum, "The interaction of scientists studying adjacent levels of organization offers the most promise for the development of marine biology."

HOWARD T. ODUM

INSTITUTE OF MARINE SCIENCE,
THE UNIVERSITY OF TEXAS,
PORT ARANSAS, TEXAS

METHODS IN CHEMICAL OCEANOGRAPHY[1]

Non-chemists in particular will welcome this volume: which constitutes the first, generally available reference and text in oceanographic chemical methods. Oceanographic departments and institutions have issued their own sets of directions for private use from time to time, and students of oceanography amass miscellaneous notes on the subject. Likewise, those engaged in water sanitation have available the APHA "Standard Methods." For the most part oceanographers have had to familiarize themselves with the vast chemical literature, adapt clinical and industrial techniques, and generally repeat one another's mistakes. Dr. Barnes' book will not, by any means, completely rectify this situation, but it should bring about noticeable improvement.

---

[1] Barnes, H. 1959. Apparatus and methods of oceanography. Part one: chemical. George Allen and Unwin Ltd., London; Interscience Publishers Inc., New York. 341 pp., 44 figs., 55 tables. 40 s, $5.75.

This is primarily a recipe book and presents the practical aspects of technique with a minimum of theory. One danger of such an approach is a tendency toward dogmatism; a tendency which the author has not entirely avoided. Thus some methods are simply condemned as "inadequate" without further comment and other methods are presented as suitable for routine use without any hint of the very real difficulties involved.

The approach is conservative; describing well-known techniques and proposing few of the author's own devising.

The first three chapters are devoted to instrumentation (photometers), a discussion of error and precision and calculation of results. All three are entirely adequate. In the chapter on error and precision there is an extended discussion of errors in glassware due to air displacement, glass expansion, etc. which are frequently ignored in routine analytical chemistry. The section on statistical analysis of results should be required reading for chemists in general, but it is not easy reading, stylistically.

The remainder of the book is given over to separate chapters on analytical methods for particular components in sea water, plankton and sediments. Each chapter is divided into sections on apparatus, reagents, technique, general discussion, and remarks. For the most part, the remarks are quite useful, being in the form of afterthoughts and comments regarding supplementary methods, alternatives and samplings. It would have been better if some of the remarks could have been included in more appropriate sections. The following are sea water components which were covered: chlorinity, pH, inorganic and organic nitrogen fractions, inorganic and organic phosphorus, silicate, organic carbon, oxygen, alkalinity, the carbon dioxide system, plankton pigments, and a number of conservative and trace elements. In addition, there is a chapter on filtration methods and one on examination of sediments.

There is one very serious omission: there is no thorough discussion of sampling techniques and problems. This is a particularly important aspect of oxygen sampling. Indeed, there is reason to believe that very little reliance can be placed on oxygen determinations made prior to 1958 with uncoated metal sampling devices, especially from great depth. The effervescing of gases from deep samples also presents problems to the analyst. Sample storage is hardly touched upon, and polyethylene bottles are condemned as unsatisfactory for storing either phosphate or nitrate samples. Apparently the author is unfamiliar with the technique of freezing samples drawn into plastic bottles. This technique revolutionized chemical oceanography in this country as it permits the actual analyses to be done on shore at the analyst's convenience. Moreover, plastic bottles are light in weight, don't break, and do not absorb ions (contrary to the author's assertion) if freezing is rapid.

One of the shortest chapters deals with a very complex subject; organic carbon in water and plankton. One of the methods (Kay's) is described as "routine," which is certainly over-optimistic. There is not nearly enough discussion of some of the very tempting but "inadequate" methods such as ceric or chromic acid titration. Weighing, instead of titrating, the evolved CO_2 is not considered. There are additional techniques which at least deserve mention. The use of B.O.D. determinations is one of these. This criticism applies as well to oxygen determinations, since amperometric and polarographic techniques are not considered.

Although both dichromate and bi-iodate standards for oxygen analysis are suggested, the two methods give different titer values for thiosulfate solutions when the suggested methods are used.

Analytical techniques are described for eight anions and cations. To judge from the dates of the references it is apparent that techniques developed later than 1954 are not included. This means that the very useful EDTA titrations for metals are not discussed. The use of dithizone on a column is prescribed for removing trace metals for analysis, but the use of exchange columns in general is not enlarged upon. For some reason the determination of sulfide is omitted.

In the past few years several rather specialized tools have been taken advantage of by oceanographers. Radiochemical procedures and the mass spectrograph have been used for example. The light spectrograph has been widely used for longer than oceanography has been a science. Although marine laboratories might not be expected to have any of these tools at hand, they should be prepared to make use of them or may be called upon to obtain samples for use in them. Therefore, there should have been some explanation of what these techniques can accomplish for oceanographers and how samples should be obtained.

The chapter on plankton pigments leaves quite a bit unsaid: nomograms are available for solving equations, membrane filters can be stored under proper conditions for long periods and can be cleared and read directly. Finally, many substances have absorption spectra similar to those normally found in plankton and could give spurious results especially when chlorophyll in sediments or "dead" chlorophyll in deep water are being sought.

There is a separate section of forty five tables in addition to ten in the text. There are both author and subject indices. The subject index is thorough and cross-referenced but hard to read. Each chapter has its own list of references, an arrangement with well-known disadvantages.

Despite these shortcomings, an untrained chemist should have little difficulty in obtaining useful results from the methods proposed. The trained chemist will find little intellectual stimulation.

HERBERT CURL, JR.
WOODS HOLE OCEANOGRAPHIC INSTITUTION

A COMPENDIUM OF OCEANOGRAPHIC GADGETS[1]

Oceanography, long a stepchild of more respectable and ancient studies, has been coming into its own in recent years. Never really neglected, the science has been the pursuit of rich dilettantes and seeming eccentrics. The extremely high cost of ship-borne research and the apparent lack of practical application of results prevented more than a handful of men from indulging their curiosity.

---

[1] Barnes, H. 1959. Oceanography and marine biology. The Macmillan Co., New York; and George Allen and Unwin Ltd., London. 218 pp., 110 figs., 35s, $7.00.

Lately, the requirements of military establishments have supplied whatever public incentive may have been lacking for massive support of oceanography. One other requirement has lacked fulfillment till now, however. This is the sufficient technological sophistication necessary to solve the very difficult problems of sampling and performing experiments in a frequently non-compliant, sometimes "hostile" environment.

Some of these problems and their present solutions have been collected by Dr. Barnes into a short, concise, well-illustrated book. It is divided into only four chapters, dealing with collecting organisms, underwater sound investigations, physical properties of sea water, and the use of photography and television.

Under biological sampling the author considers microorganisms, plankton, and benthos. The use of all-plastic sampling bottles of the Van Dorn type and the use of milli-pore filters for direct examination of bacteria, phytoplankton and plankton pigments are not mentioned. There is an extended discussion of the Hardy continuous plankton recorder, but alternative methods such as those used by S. Motoda are ignored. The latter would be of great interest to those who could not afford the seven-hundred dollar recorder. It would have been preferable to illustrate the van Veen rather than the Petersen grab from the point of view of ease of construction and use.

The chapter on the use of sound in marine research is the shortest and the best presented. As in the account on coring, there is no mention of geological applications.

Temperature, salinity and currents are considered under the heading of properties of sea water. The penetration of light is not discussed. Classical methods of measuring temperature are included and the operation of the bathythermograph with an accessory sea sampler is thoroughly discussed. The sea sampler is not in general use and does not merit description. Mention but no discussion is made of conductometric salinity determinations, a method which has supplanted titrations in many laboratories, of density determinations by precision hydrometers, and of temperature measurement by thermisters; methods all in wide use today.

It is inexplicable that the classical method of determining ocean currents from dynamic topography is not alluded to in either the section on currents or the one on temperature and salinity. Since the author has not limited himself to describing only the most recent developments in instrumentation, the use of density calculations in calculating relative currents should receive some notice. There are a variety of current measuring devices described, including drift bottles and current meters but not parachute drogues, "pop-up" buoys, and telemetering buoys.

Dr. Barnes himself has participated in investigations on the use of underwater television and the chapter on photography and television is a fairly straight-forward account of developments in this relative new field.

There is a certain amount of technical jargon which follows British usage. The author displays a fondness for complex sentences, which follow Teutonic usage, that interfere with clear exposition.

According to the author, the book is aimed at the "reading public," marine scientists, and students. It is not entirely suitable for any of these groups. The descriptions of many devices are much too detailed to constitute a popular account. Marine scientists in large institutions are already generally familiar with most of the techniques described and workers in smaller institutions will find many of the techniques far beyond their means. Students would surely benefit by becoming acquainted with some of the more ingenious "tricks of the trade" but they will have to go to a library to do so. The seven dollar price tag of of the American edition seems excessive, especially since the British edition is two dollars less for exactly the same binding.

HERBERT CURL, JR.

WOODS HOLE OCEANOGRAPHIC INSTITUTION

LIVING RESOURCES OF THE SEA[1]

The title might suggest that this is another in the growing list of books about the sea, describing its inhabitants and the fascinating variety of their adjustments to the environment. Several excellent and highly popular books of this kind have been published in the last eight years. The subtitle, "Opportunities for Research and Expansion," shows that Dr. Walford had a smaller audience in mind, those who are concerned with marine life as a resource useful to man, and who wish to know how this resource can be utilized economically to full capacity. The book is the outcome of an assignment by the Conservation Foundation to describe new research, not now in progress, that would help man to increase the harvest of the sea.

Despite these rather explicit instructions, the author wisely wove his report on the framework of existing theory, knowledge, and research effort. It demonstrates ably that a more sophisticated approach is necessary, that our concept of conservation of renewable resources must be broadened, and that in order to do this we must study many things now popularly considered to be of minor importance. Part I, "The Marine Wilderness," develops this concept and shows how human addiction to fads, so valuable to those who sell automobiles, clothing, and other expendable goods, has led to tragic neglect of certain important aspects of marine science. Investigations of the identity of species, of the dynamics of their responses to the environment, and of their behavior are among the neglected fields that should be explored. The author considers the possibility of harvesting plankton and of farming brackish waters, he stresses the importance of diseases and toxins in mortality of marine animals, he emphasizes the primitive nature of most fishing methods and the importance of improving vessels and gear.

Part II, "The Resources of the Sea," is a general survey of the principal groups of marine animals and plants, invertebrates, fishes, reptiles, mammals, and seaweeds, useful to man. It points out gaps in knowledge and suggests research that may be useful to fill them. The final chapter, "Looking Forward," speculates upon the potential harvest of the sea and points out that if we wish to exploit these resources fully we must invest much more heavily in research.

It is the reviewer's prerogative to criticise, and the book has not yet been written that can escape the critic's urge to do so. Having been associated with shellfish research for some years, this reviewer was disappointed that the fascinating story of the fungus *Dermocystidium marinum* and its role in oyster mortality from Chesapeake Bay to the Gulf of Mexico was not mentioned. This is perhaps the most completely documented case history of a marine disease of economic importance, and it would have served as an excellent example of the value of and need for such research.

---

[1] Walford, Lionel A. 1958. Living resources of the sea. Opportunities for research and expansion. A Conservation Foundation Study, Ronald Press Inc., New York. xv + 321 pp., 23 figs., tables. $6.00.

Particularly valuable are the 23 full-page world charts with detailed legends illustrating such things as the effect of weather on fishing, fertility of the sea, extent of knowledge about fishes, and distribution of whales. The book is a valuable addition to the literature of science and the sea.

J. L. McHugh

Virginia Fisheries Laboratory
Gloucester Point, Virginia[2]

---

[2] Now Chief, Division of Biological Research, Bureau of Commercial Fisheries, Washington 25, D. C.

North Atlantic Biogeography for the Biogeographer

Anyone keeping an interested eye on the rich annual harvest of biological literature is aware that this extensive crop is separable into very unevenly distributed amounts of production by the different branches of our science. That a rich harvest brings a large amount of chaff as well is natural and expected. The harvester's (reviewer's) responsibility is to try to separate the chaff from grain and try to avoid throwing out the grain.

It is particularly difficult to judge a zoogeographical treatise. Paradoxically the difficulty lies in the scarcity of such books. Casual analyses or even attempts to classify the present distribution are rare, despite our greatly increased knowledge of the necessary facts. When such work is finally published, it becomes a lonely milestone in a desert. Its proportions contrast only with the horizon and are hard to evaluate.

Recently the Swedish zoologist (the specialist in North Atlantic insect faunas) Carl H. Lindroth published a comprehensive and synthetic study of Euramerican faunal connections.[1] This problem had not been attempted by an entomologically trained zoogeographer. Therefore, the nature of the approach makes it worth serious consideration. Moreover the work is written in a fresh and personal style and is based upon a wealth of field and laboratory experience as well as on a comprehensive view of the relevant literature from both sides of the Atlantic (including the USSR). In these meritorious aspects, the book is a worthy follower of the numerous Scandinavian biogeographical-ecological monographs (Hultén, Ekman, Kalela, Økland, etc., to mention a few).

The organization of the subject matter also agrees with that of a traditional Scandinavian dissertation. The theory of Lindroth's working methods, a check list of the animals discussed (Chapter one), factual data in minute detail, a critical evaluation of the literature—all these are presented with the major conclusions and new aspects opened on the problems that the book treats.

These qualities may bother one who reads superficially, who gets lost in details about the "boats, beetles and ballast" of the second chapter. These details, however, will be a special attraction for those who really want to know how dispersal ecology in theory and in practice explains transoceanic distribution of over four hundred invertebrate species of North America.

Such a comprehensive treatment is so rare in recent English zoogeographical and ecological literature that it became welcome discussion material in the present reviewer's zoogeography seminar. It proved to be highly beneficial to and popular with students interested in this subject, mainly because of the completeness of evidence and logic in each particular presentation that Lindroth built up in the latter two thirds of the book. Those who found it difficult reading did so because of the diversity of the approach.

Zoogeography is indeed a synthetic science, and many scholars failed in solving distribution problems because of the narrowness of their grasp. It is likely that Lindroth's work can be criticized by specialists who see their particular fields from a different point of view. It is also likely that his explanation of the amphiatlantic distribution pattern is only a stepping stone toward a more final solution. But an important stepping stone indeed, one that has to be taken into account.

There are two sufficiently studied groups of biota in the North Atlantic area that may form an adequate basis for far reaching considerations. The analysis of vascular plant distribution by Hultén (1937) led to the generally accepted conclusion that European-North American specific affinities are for the most part explainable by a fairly recent Bering land bridge.

The other group comprising insects and related land invertebrates is now treated by Lindroth, although avian, mammalian and botanical evidence is also used. His main tools are comparative faunistics and dispersal ecology. Since a large number of insect species were suspected of having been accidentally dispersed by human means, he first deals with them. These cases convince the reader that the traffic of European fishermen to Newfoundland, and likely to other Atlantic ports too, served as a filter bridge carrying a large but selected group of stowaways that ecologically were capable of making the journey and of becoming established in the New World.

The species not helped by human means are sorted out into distributional geographical groups, and one by one a plausible explanation is launched for their present range. Several small species groups appear as active ocean crossers. The majority are, or have been, circumpolar, hence their occupying both Atlantic coasts. The soil-bound fauna of the North Atlantic islands presents a special problem, and Lindroth now has more evidence than in his earlier papers (E.g. in "Die Insektenfauna Islands und ihre Probleme," 1931, Zool. Bidr. Uppsala 13: 105-589) to postulate a land bridge connecting Greenland, but not Baffin Island, with the extended European continent of late Pleistocene. This theory deserves general attention and should be tested with distributional analyses of biota that speciate at a faster rate than Lindroth's carabid beetles.

---

[1] Lindroth, Carl H. 1957. The faunal connections between Europe and North America. New York: John Wiley & Sons; Stockholm: Almqvist and Wiksell. 344 pp., 61 fig., 11 diagr. $15.00.

It is natural that reading the book leaves one filled with enthusiasm and questions concerning other aspects, e.g. the ecological and taxonomical sides of the problem discussed. The questions that remained unsolved do not detract from the value of this work, especially since the author himself points out avenues of future research. To sum it up, for the biogeographer this book is a stimulating lecture and a landmark of the discipline.

MIKLOS D. F. UDVARDY
UNIVERSITY OF BRITISH COLUMBIA, VANCOUVER,
AND
UNIVERSITY OF HAWAII, HONOLULU

ZOOGEOGRAPHY[1]

In a series of articles prepared by two geologists and 13 zoologists, summaries of postulates on the origin and affinities of animals in the New World, particularly in North America, and more particularly in the region west of the 100th meridian, are presented. These essays were originally read in 1957 in symposia, one sponsored by the Society of Systematic Zoology and the other by the American Association for the Advancement of Science.

Philip B. King samples opinions of geologists on the rise of the Cordilleran system of Western North America. He evaluates theories applied to this system on marine sedimentation in Paleozoic times, land raising, folding, and faulting in later periods, and the final post-orogenic phase in Tertiary and Quaternary times when modern surface features were produced.

H. D. MacGinitie supports the contention that in North America the supposed widespread warm and even climate of the Cretaceous deteriorated throughout the Tertiary to the present conditions of decreased rainfall and increased seasonal temperature fluctuations.

George A. Bartholomew believes it is "more reasonable to look for the determinants of animal distribution in behavioral and ecological factors rather than in terms of physiological tolerances."

Donald E. Savage gives the earliest fossil record, phylogenetic affinities, and probable place of origin of 15 orders of land mammals. He summarizes opinions on the dispersal, origin, and time of origin of families of living Nearctic mammals.

William H. Burt postulates the historical movements of families of mammals into North America over the Bering land bridge.

Frank E. Peabody and Jay M. Savage suggest that the distribution of the modern herpetofauna in California might have been influenced by a marine barrier in the Pacific Coast Range during the Cenozoic.

Robert Rush Miller concludes that because of numerous and far reaching physiographic disruptions in Western North America in late Tertiary and Quaternary time, the fish fauna of the West is highly endemic, is often in isolated basins, and is depauperate.

Robert W. Pennack believes that the fresh water invertebrate fauna of Western North America lacks archaic species and is relatively depauperate because of the historic instability of the aquatic habitat in the West.

Herbert H. Ross, on the basis of phylogenies of caddisflies, sawflies, and leafhoppers correlated with suggested time chronologies, postulates that three main waves of dispersals of certain cool-adapted insects occurred in Western North America: one in middle Cretaceous, one in Paleocene, and one in Pleistocene times.

James A. G. Rehn treats the families and tribes of orthopteroid insects in North America according to their possible origin, phylogeny, and dispersal. He believes that the Sonoran region has been the outstanding center in the West for the generic differentiation of Orthoptera.

E. Gorton Linsley proposes that the cerambycid beetle fauna of Western North America is composed principally of three elements: ancient Vancouveran and Sonoran constituents and recent Holarctic elements.

William Hovanitz gives the distribution of the families, genera, and some other taxa of butterflies for all of North and South America according to latitude, climatic zone, and altitude.

Paul S. Martin attempts to explain the influence the Wisconsin Ice Sheets have had on animals and their habitats in Eastern North America. He subscribes to Deevey's school of thought that the glaciers caused the biota to be displaced far to the south. According to Martin, early man may have been responsible for the extinction of many large herbivores in post-glacial times.

Kenneth C. Parkes discusses various families of birds according to the circumstances of their possible arrival in the New World, their secondary radiation, and recent movements.

W. Frank Blair believes that the present distributional patterns of warm-adapted vertebrates in parts of North America reflect the supposed split between eastern and western forms which resulted as a consequence of Pleistocene glaciation.

Carl L. Hubbs summarizes the various opinions given by these authors.

In general the treatments presented by the zoologists, most of whom are taxonomists, are based on their extensive knowledge of the present distribution of the animals involved and their views on the phylogenetic relationships of the subjects. Records of fossils are only occasionally incorporated as evidence.

As Hubbs summarizes: "The whole volume has both the strength and the weakness that goes with diversity." Where authors stick closely to their own discipline of taxonomy, the treatments appear to be compendia of valuable information which may be referred to by other specialists for years to come. But where authors confidently endorse a supposition (historical dispersal) that needs heavy support from several other suppositions (phylogeny, past climates, possible ecological requirements of extinct animals and plants) superimposed upon a complicated, foreign discipline (geology), the result does not necessarily exemplify a happy trend in interdisciplinary research as Hubbs glowingly declares.

Time and fashion or future prejudices may make these guesses and suppositions seem shrewd or worthless and even amusing. Yet right or wrong, this book is a document of the latest thoughts of leading zoogeographers and as such it portrays the state of affairs in a section of scientific philosophy.

LEWIS J. STANNARD, JR.
ILLINOIS NATURAL HISTORY SURVEY
URBANA, ILLINOIS

---

[1] Hubbs, Carl L. (editor) 1958. Zoogeography. (Symposium) American Association for the Advancement of Science, Washington, Publication no. 51. x + 510 pp., 115 illus., 13 tables. $12.00.

Saharan Sand and Darkling Beetles[1]

In volume VIII of the UNESCO series on Arid Zone Research appearing in 1957, S. Pradhan of India commented that "few systematic efforts seem to have been made to study insect ecology or even insect distribution with special reference to arid areas." Then within a year, under sponsorship of *Centre National de la Recherche Scientifique,* Franklin Pierre published the results of a very systematic and comprehensive, though not necessarily profound, study of the ecology and entomological population of the living sands of the north-western Sahara—one of the most arid regions in the world.

His original intention had been to investigate a variety of Saharan environments. Later, realizing this procedure would lead to fragmentary achievements, he restricted himself to the most characteristic and intriguing aspect of that vast desert: accumulations of wind-blown sand, ranging from small patches and mounds to the huge *ergs* (dunes) which span immense areas. With Béni Abbès as headquarters and geographical center, he explored much of central western Algeria from the border of the Moroccan Anti-Atlas to the dreaded, excessively arid Tanezrouft in the south.

To describe the entomological population of the sands, he chose *"la méthode écologique,"* whereby the biological specializations, composition, and ecological groupings of the population were examined, from an evolutionary standpoint, in terms of decisive environmental factors. Therefore, his account of the insects—of their morphological, physiological, and ethological peculiarities and of their responses to different kinds of sands—is preceded by an equally detailed study of the environment. The climate, microclimates, and endoclimates are described as well as the essential edaphic and biotic factors.

Altogether it was an ambitious undertaking, especially under the harsh conditions imposed by the Sahara; and even though it was further restricted biologically to lay stress on the tenebrionids (qualitatively and quantitatively the most important insects of the desert), unavoidably a cursory examination of many topics resulted.

Minor irritations are lack of an index, which seems inexcusable in a book of this sort; a poor map, which the reader has to complete in order to render it usable; and a tendency to wordiness, with an excessive use of parenthetical phrases. Since Pierre is an entomologist, one wishes that he had spent more time recording direct observations on the habits of the *sabulicoles* (sand dwelling insects) even at a sacrifice of less detailed presentation of the environment. Too often in ecological studies, description of environment tends to be so thorough as to become an end in itself; whereas it should be subordinate to the account of animals or plants, with only demonstrably significant details being given.

I do not mean to imply that Pierre's volume lacks valuable information about *sabulicoles.* Quite the contrary is true. The long tables which compare, species by species, the populations of different dunes; the morphological specializations and geographical divisions of Saharan tenebrionids, etc. are a major contribution in themselves, yet take up but a small part of the section on the insect population. The weakness of the study is that many aspects had to be slighted in order to touch all phases of the remarkably well-conceived outline and list of topics. In this review, only an attenuated summary can be given of the ideas and conclusions to be found in Pierre's book, and of the wealth of information it contains about darkling beetles and the Saharan sand in which they live.

Most *sabulicoles* inhabit the upper meter (3.3 ft.) of sand, the climate of which becomes progressively more stable and tolerable towards the depths. Below 50 cm. (20 in.) there is hardly any daily variation of temperature; at one meter, the annual variation is not more than 10° C (18° F). One outstanding feature of Saharan sands, of major importance to *sabulicoles,* is high humidity. Even during summer, the air surrounding loose dry grains at a depth of only 50 cm. (20 in.) has a relative humidity of 50%. This moisture rises from extra-Saharan water which underlies most of the dunes, occurring at 5 to 25 meters (16-82 ft.) in the Great Western Erg. Often the uniformity of the internal climate of the sand is broken by distinct microclimates. Immediately under a stone the temperature is about the same as at 10 cm. (3.9 in.) below a bare surface; it also shows less daily variations.

The distribution of many species of *sabulicoles* must be explained on the basis of edaphic factors, of which grain size is of paramount importance. It determines degree of rigidity, cohesion, and mobility as well as the capacity of the sand for air or water. Except in particular places, decomposed organic material, calcareous deposits, and salts are scarce. One exception is under tamarisks, whose salt-excreting leaves render the sand so cohesive as to be unfit for *sabulicoles.*

Directly or indirectly, populations of *sabulicoles* depend upon the vegetation, decreasing in amount from north to south. In parts of the Great Western Erg, density of plants compares with that of the Algerian plains, but in the Erg Chech five to twenty kilometers (3-12½ mi.) separate clumps!

Approximately 200 species and subspecies of insects representing 12 orders (out of some 800 kinds and 26 orders in the north-western Sahara) are associated with the sands. They can be classified ecologically on the basis of distribution, frequency of occurrence, and qualitative rank in different types of sand. Two major groups are then seen to exist. One is the fauna of the *ergs,* similar between dunes and progressively impoverished towards the south; the other is the fauna of isolated mounds and patches of sand.

The distinct morphological, physiological, and ethological specializations of many of the xerophilous *sabulicoles* represent a stable condition achieved in an ancient and severe environment. Even cave dwelling insects do not show greater adaptations to their particular situation. Morphologically, the main characteristics are an excessive development of certain organs, notably legs and sensilla. Other features, many of which are illustrated in the book, are pseudophysogastrism (apparent enlargement of abdomen); apterism; hypertrophy of tibia, nail of anterior foot, and elytron; an air and water tight subelytral cavity; and black tegument, which affords protection from ultraviolet rays.

Among physiological peculiarities of *sabulicoles* are aptitude for fasting, strong resistence to desiccation, and non-tolerance of high temperatures. All but three of the forms observed avoided surface temperatures of from 30° to 50° C (86°-122° F). One device by which

---

[1] Pierre, Franklin. 1958. Écologie et peuplement entomologique des sables vifs du Sahara Nord-Occidental. Paris: Centre National de la Recherche Scientifique, Publications du Centre de Recherches Sahariennes, Série Biologique No. 1. 332 pp.; 140 figs., 16 plates, 35 tables. 3,200 fr., $9.25.

sabulicoles seem to overcome relatively high temperatures is a pseudo-regulation of body heat through evaporative loss of water proportionate to rise of ambient temperature.

The most effective ethological adaptation to the sand and the usual means of escaping lethal temperatures is burrowing. The "true burrowers" are those *sabulicoles* which swim through a loose substratum without making a hole, while "excavators" dig pits in similar places, and "miners" require cohesive sand in order to construct tunnels.

By the time the reader of Pierre's book reaches the chapter which discusses the structure of ecological groups, he will realize that unquestionably and at long last a systematic study of ecology and distribution of insects in an arid region has been made. Also, by then he should be well aware, if he was not already, that the popular notion of lifeless Saharan sands is erroneous. A recent article in NATIONAL GEOGRAPHIC MAGAZINE (113: 664-705) said of the Great Ergs: "Nothing lives in those desolate worlds of drifted sand—not a beetle, a blade of grass, or, strangely enough, even a fly!" As to the origin of the extensive insect population which does live there, Pierre believes that it stems from a high rate of endemism augmented not so long ago by a tremendous influx of already specialized forms from Asia.

LLOYD TEVIS, JR.

DIVISION OF BIOLOGY
CALIFORNIA INSTITUTE OF TECHNOLOGY
PASADENA, CALIFORNIA

MAN AND THE LAND: TWO DISCUSSIONS[1,2]

The inauguration in recent years of a new concept of function, style and design for the Yearbooks of the United States Department of Agriculture has resulted in a shelf of great value to the working ecologist. At least one issue has become virtually a collector's item, not safely to be left unguarded, as this reviewer knows from experience. The current volume,[1] essentially a reference book on the basic problems of land use, continues to maintain the high standard of exposition, information and illustration we have become accustomed to expect.

The book begins with nearly fifty pages of historical-geographical cuts of excellent quality and interest. Then follow ten chapters, each conveniently subdivided into numerous sections. Inventory, description, analysis and forecast are taken up in sequence, with description and analysis given the bulk of space. More than ninety authors have been involved and of these a considerable number have contributed more than one section. Yet the general smoothness and balance reflect great editorial skill and, let us hope, a considerable meeting of minds.

Valuable as the review of what we have, its capabilities and how we got it undoubtedly is, the crux of the volume is in its discussion of policy in the light of present trends and future needs. The rapid alienation of productive land for urban and related uses, the achievements and possibilities of technology, and the certain increase of demand for products of the soil are given due attention. The general tone is one of cautious optimism, with frequent reminders that cooperation from a responsible and informed public will be increasingly necessary.

Knowing as we do the handicaps under which our civil servants must work, we cannot censure them for a certain restraint in dealing with such troublesome fundamentals as the finite quantity and quality of our space and the need to face squarely the question of uncontrolled population increase. Yet we can be grateful for the refreshing frankness with which, for example, Mr. Mason Gaffney deals with urban expansion. He poses three questions: Are efficient cities evolving? Are cities swallowing much more farm land than they need? Does present urban expansion involve the kind of instability which has in the past brought collapses? His answer to each is disturbing and in my judgment sound.

The concluding chapter that follows his section presents many thoughtful suggestions for planning and clearly acknowledges the principle of balance. Thus what is clearly an ecological document ends on a sound ecological note, even though the rubric of that science does not appear in the index and, if present in the text, has escaped my eye.

Of especial interest is a brief, well illustrated section on air photos and their value in land-use analysis.

The symposium presented in THE POPULATION AHEAD,[2] as explained by the editor, had the dual purpose of encouraging not-too-technical interchange between experts in different fields and of clarifying an urgent problem—that of "optimum" population or "optimum population growth." Held in 1957 under the auspices of the University of Minnesota, its 8 participants and 5 commentators have been under no visible inhibitions. The net result is a frank and illuminating interchange of expert knowledge that supplements the other volume under review, for assuredly it is the growing pressure of population that gives to land use problems their immediacy.

In view of the active discussion in this field and the strong opinions now being expressed with greater vigor than ever before, it is good to note the temperate tone that pervades the book. Evidence is allowed to speak for itself, without fatuous optimism or pessimistic gloom. And, in the tradition of the best of modern social science, there is a thread of agreement that the problem of population and its adjustment is basically one of values rather than technologies.

This emerges, not by obscuring the biological and ecological components, but rather from giving them full consideration. Whelpton, acknowledging the present population explosion and its seriousness, discusses the demographic revolution whereby reduction in death rate is followed sooner or later by reduction in birth rate, leading to eventual equilibrium.

Keys, rightly pointing out the difficulty of fixing optimum population size, shows that at least an optimum rate of increase can be dealt with. This is important, in view of the demonstration by Spengler and others that beyond a certain point urban increments are liabilities rather than assets. The problem may thus not be so much one of absolute limits as one of digestion—not biting off more than can be chewed and swallowed without danger to health.

[1] Stefferud, Alfred (editor) 1958. LAND: The Yearbook of Agriculture 1958. (Symposium) United States Government Printing Office, Washington, D. C. xi + 605 pp. Num. figs., tables. $2.25. From Superintendent of Documents, Washington 25, D. C.

[2] Francis, Roy G. (editor) 1958. The Population Ahead. (Symposium) University of Minnesota Press, Minneapolis. x + 160 pp. $3.75.

Broek, in showing that the land-man ratio must vary with the type of culture, questions whether a strictly economic measure is possible or desirable. It would have been interesting to have had his comments on such recent suggestions as those of Galbraith and Ordway that a less consumptive economy than our own might afford great human satisfactions as well as greater permanence.

There are two excellent biological chapters, by Deevey and Sax respectively. The former, after showing that the subsistence pyramid must be telescoped to a vegetarian diet if population becomes too dense, gives impressive evidence of implicit mechanisms that tend to regulate population. Sax is characteristically concerned with developing adequate safeguards of genetic quality, and quotes Muller's reminder that the chief concern in planning parenthood should be the welfare of the descendants themselves.

Spencer's paper develops explicitly the theme already noted—that in the last analysis it must be through the values of a culture that its population is regulated.

The final chapter, by Harberger, turns out to be the most controversial, as the final discussion indicates. It is also the most definitely optimistic. On the basis of formulae which he presents he suggests that any population, by the proper employment of technology and capital, should be able to take care of any increase that it allows to develop, although he grants that it may not choose to do so.

The valuable concluding commentary, ranging as it does over the entire symposium cannot be summarized here, but should be read for its own merit.

Paul B. Sears

Yale University Conservation Program

Tropical Ecology[1]

It is frequently remarked, and probably with reason, that ecological principles, as developed in the temperate zone, may be of dubious application in tropical environments. Much scattered ecological work has been done in the tropics, but most of it has been done on short visits or on expeditions by workers with a temperate-zone orientation. Only recently has work of an indigenous character commenced in tropical countries. Very few attempts have been made to review and generalize the results of work in the tropics, or to determine if principles apply comparable to those elucidated during the past 75 years in temperate ecology. Much less have there been indigenous text books written by ecologists residing in tropical countries. The work reviewed here, written by two of the most active and productive of the Indian ecologists, is a first attempt to produce a comprehensive text and reference work on tropical plant ecology for the use of tropical ecological students.

This is an important work in many respects, in addition to being the first in its special field. It illustrates, among other things, the present inadequacy of available data on many aspects of ecology in the tropics and the dependence on temperate zone results. Repeatedly, illustrative material is drawn from European and American work. Fortunately the authors have, themselves, worked in Europe and their utilization of European data is done with considerable understanding. In spite of these facts, however, not the least important feature of this book is the bringing together of the available information and bibliography on tropical plant ecology, especially on the work done in India.

As with all authors of ecological texts, the writers of this one have had to face the dilemma of which to describe first, the plant community or the environment. Neither of the obvious solutions can be regarded as a particularly happy one, but perhaps the one chosen here, of placing a mixture of autecology of plants and the basic principles and methods of study of the synecology of communities first and detailed analysis of environment last is as good as any.

The idea of regarding the environment as a series of interacting systems is a particularly good one and could have been profitably extended to the biotic communities also. The approach to understanding of the nature of plant communities is basically Clementsian, while the methods of study described and recommended are mainly European. In general, however, in both interpretation and methodology, abstract ideas are avoided and the tone is definitely "down-to-earth," perhaps almost too much so. It may be that students, going from a training based on this book to the general literature of ecology will experience a shock to find that there are still many areas of deep philosophical disagreement between ecologists, especially on the nature of biotic communities and the validity of the methods used to study them. But again, perhaps it is better to let students find these things out for themselves, rather than to dwell on them in elementary texts.

In the chapters devoted to the several environmental systems and factors a useful feature is the inclusion of very simple definitions and discussions of some of the basic concepts borrowed by ecology from related sciences which are glibly used by ecologists though not always understood by them. Such are *base exchange*, p. 172, *redox potential*, p. 152, *mull, mor, raw humus* and *peat*, pp. 122-130, *relative humidity* and *saturation deficit*, p. 315, and many others. A few of these explanations may be too simple, or even not thoroughly understood by the authors, but in general they will be very useful for students.

Throughout the book an attempt has been made to present illustrative material in tabular form. This is effective except in some places where the meaning or application of the tables is not clear or where the tables are too complicated. Many maps are used, most of them rather too small to be very effective in bringing out correlations. Much attention is given to the various systems of classification of climate, their development, and correlation or lack of it with vegetation patterns. They are illustrated with maps and various sorts of climatic diagrams which are, in general, too much reduced to be of much value. It is valuable, however, to have these systems summarized and contrasted as they are here, even though in some ways the summaries are too brief to be altogether clear. The chapter on the Climate of India will be a useful reference for non-Indian ecologists and plant geographers as well as for those for whom it was primarily intended. The same may be said for the corresponding chapter on soils, as well as for the smaller or more scattered sections summarizing other factors for India.

---

[1] Misra, R., and G. S. Puri [1958]. Indian manual of plant ecology. The English Book Depot, Poona-1, India. x + 341 + xiv pp., 56 figs., 111 tables. 15.50 rupees ($5.00).

In general, one can say that the concept of this book is as adequate as that of most ecology texts, though this may not be much of a recommendation. The concept has been carried out in perhaps as coherent a fashion as could be expected in a first edition covering as vast a field as plant ecology. Many improvements will certainly be made in a second edition, but the authors are to be commended for their achievement in providing a basis for the teaching of the subject in India and a very useful reference for other tropical countries.

One wishes he could say as much for the editing. Seldom has the reviewer encountered a book so poorly edited. In fact, one might almost say that it probably has not been edited at all. The diction and grammar are about those of a rough draft. One cannot criticize the authors for poor writing in a language not their own, but surely it would have behooved the publisher to see that the manuscript was corrected by an editor thoroughly conversant with English usage. This is common and necessary practice even in countries where nothing but English is spoken. The attention of users is especially directed to the five pages of *errata* at the end of the book.

The indexing is quite inadequate. The paper is bad and the printing not very good. And an abominable English habit has been followed of having no date on the title page. Judging from the dates on foreword and preface the writing was completed in 1954. When the book was published is anyone's guess.

On the other hand, compared with American texts, the price is very reasonable. At 15.50 rupees the book should be within the reach of most students and therefore may be expected to exert a major influence on Indian ecology during the next generation.

F. R. Fosberg

Falls Church, Va.

A Vegetation Map of Africa[1]

Under the auspices of the Commission for Technical Co-operation in Africa South of the Sahara/Scientific Council for Africa South of the Sahara, a meeting was held during 1956 at Yangambi in the Congo Belge to draw up a common system for the nomenclature of African vegetation classified on the basis of physiognomy. C.S.A. Publication 22 records this meeting which was also briefly reported in Nature, Lond. 178, 1273-1274 (1956).

This map, which is subsidized by UNESCO, was produced by the Association pour l'Étude Taxonomique de la Flora d'Afrique Tropicale because its members required a vegetation map for their taxonomic work. To prepare this map, A.É.T.F.A.T. set up an editorial committee, one of whom (Mr. Keay) has written the explanatory notes which appear in English and in French translation by M. A. Aubréville. This committee has, with occasional exceptions, used the Yangambi nomenclature system for vegetation. (The erroneous spelling savannah occurs on page 7 of the explanatory notes to this map: elsewhere the recommended spelling savanna is used.) There is also a good bibliography.

Since the pioneer work of Shantz and Marbut in 1923 no attempt has been made to map the vegetation of Africa as a whole. Maps of the vegetation of various parts of Africa have been prepared but these were intended for various purposes and have different emphases. Also they are not all on the same scale. The present map shows, with the exception of cultivated areas, "the vegetation as it is today, and not the presumed climax types." Local experts prepared maps of their countries which were co-ordinated into a homogeneous whole by the committee.

So much for history and methods; what of the finished map? This is on a scale of 1:10m. and is therefore folded into twelve and contained in the end pocket of this work. (Unfolded maps for wall display, together with the explantory notes, may be obtained on special application to the Oxford University Press.) It is coloured and on the zenithal equal-area projection. Cartographically it is very good and up to the high standard expected from the Clarendon Press. The general distribution of the vegetation types can be seen at a glance.

The vegetation types, which are numbered 1-32 for convenience, are mapped in 16 colours, each colour representing one, two, or three similar types. In addition large areas of SWAMP and *Oxytenanthera* BAMBOO THICKET are shown as overprints. MANGROVE vegetation is, for some curious reason, shown as an additional (unnumbered) colour.

The vegetation types have been arranged in such a way that similar ones can, if necessary, be grouped together for mapping. For instance the MONTANE COMMUNITIES—UNDIFFERENTIATED type is used for three purposes: montane areas containing several types of vegetation which are too small to map separately; montane areas which are not well known; and diverse montane communities which do not easily fit into any other class. The same could be said of the WOODLANDS, SAVANNA (AND STEPPES)—UNDIFFERENTIATED—RELATIVELY MOIST (or DRY) TYPES. This procedure has greatly simplified the task of mapping even if it somewhat blurrs the general picture.

Experts, looking at the vegetation of their own regions, will undoubtedly find causes for complaint. Even in Nigeria, which was contributed by Mr. Keay, the position of some boundaries might be questioned. (The MONTANE EVERGREEN FOREST on Cameroon Mountain should surely be MONTANE COMMUNITIES—UNDIFFERENTIATED?) As some regions are more intensively mapped than others, the detail on this map varies. However, when it is remembered that this is a map which is intended to be looked at as a whole, these criticism become quite minor.

Ecologists are naturally sceptical of ecological work done by taxonomists. With the exception of the inclusion of the MONTANE COMMUNITIES—WITH AFRO-ALPINE COMMUNITIES type (which is only slightly different from the MONTANE COMMUNITIES—UNDIFFERENTIATED type) ecologists can allay their fears on this score. What is open to question is not so much the mapping itself as the system of vegetation classification behind it. A physiognomic basis for vegetation classification is sound for the major divisions which themselves may be subdivided on other (floristic, habitat, etc.) criteria. A fundamental approach to the objective classification of African vegetation is required. It would yield interesting and valuable results.

---

[1] Keay, R. W. J. 1959. Vegetation map of Africa south of the Tropic of Cancer (with French transl. by A. Aubréville). Oxford University Press, London and New York. 24 pp., 1 coloured map. 15s, $2.40.

The most disappointing part of this map is that, although it includes Madagascar, it does not include the area north of the Tropic of Cancer. The reason for this is presumably that the project was backed by bodies concerned with tropical Africa or with Africa south of the Sahara. Nevertheless it is a great pity that this northern strip of the continent was unmapped. A second edition should include this area even though a few more vegetation types may have to be added.

The vegetation of Africa south of the Sahara can now be seen on a good map which will be useful not only to plant ecologists but to many other biologists and geographers.

BRIAN HOPKINS

UNIVERSITY COLLEGE
IBADAN
NIGERIA

PRACTICAL PHENOLOGY[1]

Unintentional introduction of plants to new areas is as old as the first movements of human beings from one place to another, and intentional transport of cultivated plants has characterized mankind since the beginning of agriculture. Intensified agriculture has made it necessary to increase such introductions very greatly in recent decades, but although botanical sciences in general and geobotanical approaches in particular ought to have formed the basis for these improvements in the cultivated floras, most intentional introductions still are based more on good notions than on real knowledge. The reason for this may often be that phenological information is not always easily available for all areas of interest, or is too limited and based on plants of little importance to those concerned with the introductions.

It is probably not universally known that in Washington, D. C., there is an American Institute of Crop Ecology, which for a period of many years has been making studies on agricultural climatology and phenology of many areas in the Old and New Worlds. This Institute has published a number of books on the results obtained, the last two of which, printed in 1957, report on rye-climate and barley-climate relationships. Since these books are filled with information in tabular form, they cannot be described in detail, and their conclusions based on these compilations are beyond discussion. But there can be no doubt that the twenty books already published by the Institute are among the most valuable manuals available in any language for those who plan to introduce cultivated plants into new areas. And plant-breeders, who desire to collect additional material, also can get here all the detailed information needed to secure the greatest success of their selections. Last but not least, it is also very likely that ecologists interested in aspects other than the practical ones may find much relevant material in these books, and profit from methods which have perhaps been forgotten in some ecological studies of recent times.

ÁSKELL LÖVE

INSTITUT BOTANIQUE
UNIVERSITÉ DE MONTRÉAL

---

[1] Nuttonson, M. Y. 1957. Rye-climate relationships and the use of phenology in ascertaining the thermal and photo-thermal requirements of rye. Based on data of North America and of some thermally analogous areas of North America in the Soviet Union, Finland, Poland, and Czechoslovakia. American Institute of Crop Ecology, Washington, D. C., 219 pp., 17 figs., 87 charts, num. tables.

Nuttonson, M. Y. 1957. Barley-climate relationships and the use of phenology in ascertaining the thermal and photo-thermal requirements of barley. Based on data of North America and of some thermally analogous areas of North America in the Soviet Union, Finland, Poland, and Czechoslovakia. American Institute of Crop Ecology, Washington, D. C., 280 pp., 15 figs., 124 charts, num. tables.

THE PHOTOCHEMICAL ORIGIN OF LIFE[1]

In the last decade, it has become not only possible but imperative for physical and biological scientists to enter into serious discussions on the origin of life on earth. The appearance of a book with this title by A. I. Oparin in 1936 led to a good deal of serious thinking and review of biogenetic hypotheses. Many of the recent developments in biochemical genetics, virus research and the chemistry of nucleic acid and proteins, have centered about numerous stimulating theories on the manner in which life could be presumed to arise from non-living precursors. In the past few years numerous articles on this subject have appeared in popular publications, symposia have been held at many national meetings, and articles have even found their way into the local newspapers. The present reviewer recalls vividly lecturing on this subject before a sophomore biology class some years ago, and running into either enthusiastic interest or stolid rejection of such thinking, mostly on religious grounds.

A. Dauvillier is a professor at the College de France and is director of a laboratory of cosmic physics of the Observatory of the Pic-du-Midi. He has previously written books on such topics as the "Genesis, nature and evolution of planets," and on related astronomical and cosmological problems. In this book he attempts to extend the sphere of his interest to the biological world. In a sense, the title is misleading, for Dauvillier covers much more ground than the question of the photochemical origin of life.

The book opens with an introduction reviewing theories on the origin of life, and providing information on some of the basic numerical constants required in the subsequent treatments. The first chapter deals with the nature of living matter, its chemical composition, the nature of macromolecules and of some of the other important cellular components. The author shows in this treatment a reasonable understanding of the nature of biological systems, but makes a few naïve errors that show that he is not a biologist. For instance, he refers to ATP as a constituent of ribonucleic acid, though on the very next page he correctly shows that adenine is present as the nucleotide. This first chapter closes with a discussion of the effect of temperature and of radiation on living matter. Chapter 2 deals with theories on the origin of life, including spontoneous generation, cosmic panspermy, and chance as a creative force. Chapter 3 deals with cosmogony and the origin of the earth. In this discussion are included discussions on the origin of the universe, of the solar system, and of the earth itself. Chapter 4 deals with the origin of continents, oceans, and atmospheres. It includes a discussion of the chemistry of the lithosphere, the synthesis of organic compounds at high temperatures, the origin of the oceans, the origin of the primitive marine milieu, and the origin of the atmosphere. Chapter 5 deals with the photochemical synthesis of organic matter, including a discussion of the energy of various radiations, and the syntheses possible by each of the radiations. In photosynthesis proper, the author considers some aspects of the chemistry of carbohydrates and of other organic molecules. Here again, he shows that he is not completely at home, by giving serious credence to the long discarded diketopiperazine theory. In this chapter he considers the work of Stanley Miller on the origin of amino acids in discharge tubes, and the origin and significance of optical activity in the living world. Chapter 6 is a consideration of the organization of organic matter and the evolution of living things. Here he attempts to cover much basic biochemistry, and makes a few naïve statements. For instance, on page 143 he states that the Pasteur effect is known to be due to an interference with an enzyme which transfers phosphate radicals from ATP to fructose-6-phosphate. This reviewer was not aware that the situation was so clear. However, in its broad outline this chapter is useful and even excitingly written. Photosynthesis, chloroplasts, chlorophyll pigments, and a variety of other topics are treated briefly. The general subject of organic evolution is treated so briefly as to be practically without meaning; but provided one has a background in biology, it is useful to see how this subject looks from the point of view of a physical scientist. Chapter 7 deals with the energetics of the biosphere. Here the author discusses the efficiency of biological energy transformations compared with that of mechanical systems. He shows adequately the competence of living organisms and sets in its proper place the relationship of the laws of thermodynamics to living systems. Chapter 8 concerns the geochemical role of the biosphere and details some of the cyclical chemical changes produced on earth as a result of the action of living beings. Chapter 8, Life in the Universe, is a consideration of the other planets of the solar system and other terrestrial bodies on which life may be supposed to exist.

---

[1] Dauvillier, A. 1958. L'origine photochimique de la vie. Masson et Cie (Évolution des Sciences N° 11), Paris. 211 pp. 1,300 fr. ($3.80).

It might be useful to close this review by translating the last paragraph of the book. "Life and thought are perpetual only in a statistical sense, and play no role in the dynamic evolution of the universe. Life appears, evolves and disappears on a myriad of planets according to a cycle billions of years long, limited in time by cosmic accidents or by the effect of its own evolution."

All in all, this reviewer found Dauvillier's book to be an interesting synthesis of many of the exciting scientific findings of the last 50 years or so, all of them focused on one of the greatest mysteries we have to face, the nature of the processes which led to the origin of life on earth.

ARTHUR W. GALSTON

DEPARTMENT OF BOTANY
YALE UNIVERSITY

CORRECTION

In the paper "Flow, temperature, solar radiation, and ice in relation to activities of fishes in Sagehen Creek, California" by P. R. Needham and A. C. Jones, Ecology 40 (3), 1959, on p. 473, column 1, line 15, read "lotic" instead of "lentic."

INDEX TO ECOLOGY, VOLUME 40, 1959

A

Abbott, D. P., reviewed, 328
Abell, D. L., article, 186
Acer saccharum growth, 261
Acer saccharum leaf litter, 485
Acid treatment in germination, 21
Acoustic orientation, review, 527
Adams, Hazel B., note, 717
Adams, Lowell, and Hazel B. Adams, note, 717
Adrenal, weight in chickens, 495
Aeration in tobacco germination, 631
Aeration of reference sample in CO_2 measurement, 322
Africa, Kenya, 490
Africa, vegetation map of, review, 754
Age structure, and sex in roosting starlings, 136
Agricultural ecology, reviews, 331, 755
Agropyron spicatum, 674
Air pollution effects on *Lupinus,* 620
Alaska, interior, soils, 492
Algae in chemical solutions, 732
Algae: the Grass of Many Waters, reviewed, 526
Algal establishment in sterilized soil, 474
Allen, George H., article, 108
Alpine snowbank environment, Wyoming, 388
Alpine zone vegetation, 12, 16
Analysis, chemical, of plant material, 646
Anatidae, learning in young, 90
Andropogon gerardi in Oklahoma, 255
Andropogon scoparius, 255
Andropogon spp. in Wisconsin prairies, 37
Animal behavior, review, 526, 527
Animal Ecology and Demography, reviewed, 325
Animal Ecology Today, reviewed, 326
Annual rings, missing, in Douglas-fir, 480
Anopheles quadrimaculatus, development in Georgia winter temperatures, 198
Ants, in New Guinea rain forests, 437
Apparatus and Methods of Oceanography, reviewed, 746
Aquatic organisms, passive overland transport of, 321
Arctic lake limnology, 49
Arid Zone, a newsletter, reviewed, 530
Aristida stricta, storage in roots of, 292
Arizona, 626
Arizona, epiphytism in desert of, 324
Arizona rangeland, 738
Artemisia frigida, 270
Artemisia nova, 644
Arnold, C. A., note, 146
Ascia monustel, temperatures preferred, 181
Atoll, review, 328
Atriplex canescens, 644
Atriplex confertifolia, 644
Aubreville, A., reviewed, 754
Augmented variable-radius method, 597
Australia, grass competition in, 141
Australia, soil and eucalypts in, 734
Australia, soil nutrients in a section of, 337
Australorbis glabratus, physiochemical environment, 533
Avalanche-type landslides, 692
Azzi, Girolamo, reviewed, 331

B

Bach, Roman, reviewed, 330
Bacteria, marine, 711
Baloghn Janos, reviewed, 520
Balsamorhiza sagittata, 674
Bardach, John E. and Howard E. Winn, note, 296
Barley-climate Relationships and Phenology, reviewed, 755
Barnes, H., reviewed, 745, 747
Barnstable Marsh palynology, 735
Bates, Marston, reviewed, 328
Bats, acoustic orientation of, review, 527
Behavior, animals, reviews, 526, 527
Behavior, in chinook and silver salmon, 108
Behle, W. H., reviewed, 528
Belgium, soil zoology in, review, 168
Benton, A. H., reviewed, 327
Bess, Henry A. and Frank H. Haramoto, article, 244
Billings, W. D., articles, 16, 388
Biogeography, reviews, 749, 750
Biotope, concept of, 724
Bird Life of Great Salt Lake, reviewed, 528
Black Widow, habits and venom in Israel, 515
Blight, chestnut, aftermath of, 349
Bliss, L. C., article, 388
Blueberry stands in New Brunswick, 742
Bobcoat of North America, reviewed, 528
Bodenheimer, F. S., reviewed, 326
Bog, reverse succession in, 317
Bormann, F. H., article, 677
Botany and plant ecology, 153
Bothriochloa ambigua relation to Danthonia, 141
Bourdeau note, comment on, 738
Bourdeau, P. E., note, 148, article, 63
Bovbjerg, Richard V., note, 504
Box, Thadis W., note, 714
Boyd, W. L., article, 49
Brackish water swamps, tropical, 708
Branchiobdellids, survival without host, 514
Braun-Blanquet, J., reviewed, 330, 523
Brazilian campos, sulfur deficiency in, 315
Brewer, Richard, review, 528
Brink, V. C., article, 10
British Columbia timberline ecotone, 10
Bromus carinatus, 675
Bronson, Franklin H. and Otto W. Tiemeier, article, 194
Brooks, J. L., reviewed, 529
Bryan, Arthur H., note, 711
Bryan, Charles A., note, 711
Bryozoa, seasonal distribution and settling rates of estuarine, 116
Budworm, spruce, 608
Buell, M. F., note, 317
Bufo punctatus, ecology of in Death Valley, 175
Burbanck, W. E., note, 507
Burt, Wayne V., W. Bruce McAlister, and John Queen, note, 305
Butler, Patrick, note, 735
Buzzati-Traverso, A. A., reviewed, 745
Byer, M. D., note, 323

C

Caldwell, R. E., article, 292
California, 621, 626
California, mosquito populations of foothill stream in, 186
California, shell formation and growth in xanthid crabs, 113

Callinectes, extremely small ovigerous, 719
Campos, Brazilian, soil deficiencies of, 315
Canada, New Brunswick, blueberry stands in, 742
Canada, spruce budworm outbreak areas in national parks of, 608
Canopy openings in Piedmont pine forests, 478
Cantlon, J. E., note, 323
Cape Cod, Mass., palynology, 735
Carbohydrates in roots, 292
Carbon dioxide determination in water, 322
Carex spp. in frost effects, 16
Carnegiea gigantea, and epiphytic prickly pear cactus, 324
Carya ovata leaf litter, 485
Castanea dentata replacement, 349
Cenchrus pauciflorus, 270
Centipedes, natural history of, review, 167
Chemical content, desert plants, 644
Chemical solutions (lab) as alga habitats, 732
Chestnut, replacement in Appalachians, 349
Chiang, H. C., note, 310
Chickens, adrenal weight and crowding, 495
Chipman, Robert K., note, 299
Chironomidae, production, 425
Chitty, Dennis, note, 727
Chlorophycaceous alga in laboratory chemicals, 732
Choristoneura fumiferana, 608
Christmas, J. Y., note, 723
Chrysothamnus nauseosus, 268
Chrysothamnus stenophyllus, 644
Chub, ecology of, 564
Cionella lubrica, distribution, 447
Cladocera, reproduction and illumination, 514
Classification of swamp communities, Papua, 703
Clausen, Jens, reviewed, 519
Climate, postpluvial, in Utah, 361
Climatic change in Adirondacks, transect for study of, 320
Claudsley-Thompson, J. L., reviewed, 167
Coastal Sand Dunes of Oregon and Washington, reviewed, 332
Cold Spring Harbor Symposium on population ecology, review, 325
Coliform organisms in arctic lakes, 51
Collis-George, N., article, 550
Comandra umbellata, 674
Community organization, and species abundance, 404
Competition and purslane, 666
Competition between Bothriochloa and Danthonia, 141
Competition in root systems, 271
Conifer photosynthesis, 738
Conifers, photosynthetic efficiency in, 63
Conservation, reviews, 752
Contagious distributions, 447
Containers for increment cores, 148
Content, chemical, of desert plants in winter, 644
Continuum, forest, in Oklahoma, 598
Convolvulus arvensis, density of, 732
Cook, C. W., article, 643
Cook, D. B., article, 333
Cook, S. F., Jr., article, 102
Cooke, W. B., article, 273
Cooper, W. S., reviewed, 332
CO_2 production by phytoplankton, 377
Coquinas, distribution on Florida beach, 498
Coral Island, reviewed, 328
Coral Reefs, ecology of Jamaican, 67
Corixid insects in sea, 723
Corn borer, mortality factors, 310
Cottam, W. P., article, 361
Cotter, D. J., article, 651
Cover measured by loop frequency method, 668
Crabs, extremely small ovigerous, 719
Crabs, shell formation and growth in, 113
Crasperacusta sowerbii, effects of temperature on, 158
Croton texensis, 268
Crowding, effect on adrenal weight in chickens, 495
Crown cover measurements, 668
Cryptozoa, fit of distribution functions to, 447
Cupressus lusitanica, log temperatures, 490
Curl, Herbert, Jr., reviews, 746, 747
Curry, S. J., note, 490
Cyathura (isopod), distribution, 507
Cybernetics of the ecosystem, 221
Czarnowski, M., note, 312
Czechoslovakia, 732

D

Dalea scoparia, 269
Dalton, P. D., note, 738
Dansereau, Pierre, reviews, 521, 523
Danthonia spp. in Australia, 141
Daphnia pulex, populations, 232
Daphnia, systematics of, review, 529
Dauvillier, A., reviewed, 755
Davis, C. C., review, 526
Davis, David E., artcile, 136
Death Valley, ecology of *Bufo punctatus* in, 175
Deficiency of sulphur in a Brazilian soil, 315
Deformities, in fishes inhabiting warm springs, 154
DeFrietas, L. M. M., note, 315
Demography, review, 325
Density estimation, 732
Deposit areas for landslides, 697
Deserts, insects of, review, 751
Dexter, Ralph W., note, 507
Distribution functions, fitted to counts of cryptozoa, 447
Distribution of Nicotiana and ecological factors, 626
Dittmer, H. J., article, 265
Dix, R. L., article, 36
Donax variabilis, distribution on Florida beach, 498
Douglas fir branch growth, 480
Doutt, Richard L., note, 302
Drobnick, R., article, 361
Drought effects on Oklahoma forests, 604
Drought response in a purslane, 661, 662
Drought, soil vs. atmospheric, 640
Dugdale, Richard C., article, 425
Dunn, D. B., article, 621
Dye injection and movement in trees, 678

E

Ecological life histories of *Nicotiana* spp., 626
Ecologie et Peuplement Entomologique des Sables Vifs du Sahara Nord-Occidental, reviewed, 751
Ecology of Invasions by Animals and Plants, reviewed, 168
Ecosystem including desert tobaccos, 641
Ecosystem of a trickling filter, 273, 289
Ecosystem traits, spruce budworm areas, 608
Ecotone, forest-heath, in British Columbia, 10
Edgren, Richard A., note, 498
Egg distribution, of *Microbracon,* 302
Eggs, delayed hatching in *Fundulus,* 430
Eleocharis spp., 4
Elton, Charles, reviewed, 168

England, R. B., note, 474
Eosinophil, responses of mice to behavioral disturbance, 156
Ephedra nevadensis, 644
Ephestia-idechthis, ecosystem delimited by vermiculite, 165
Epiphytic prickly pear on saguara, 324
Eradication season related to root reserves, 295
Eragrostis lehmanniana in Arizona rangeland, 738
Eubranchipus holmani, biology of, 398
Eucalyptus melliodora, 734
Eucalyptus rossii, 734
Eucalyptus spp. and soil, 734
Eucalyptus spp. associations, 339
Eupatorium adenophorum, control of in Hawaii, 244
Eurotia lanata, 644, 673
Everglades vegetation, 1
Evolution as a process, reviewed, 529
Excerpta Botanica, Sectio B: Sociologica, reviewed, 530
Experimental studies on the nature of species, reviewed, 519

F

Fagus grandifolia growth, 263
Fairy shrimp, biology of, 398
Faunal connections between Europe and America, reviewed, 749
Feder, Howard M., note, 721
Fence row cover and mammals, 140
Festschrift Werner Lüdi, reviewed, 328
Fiddler crabs, thermal death limits, 589
Field Biology and Ecology, review, 327
Filter, trickling, ecology, 273
Fire, effects on a population of small rodents, 102
Fire, forest fires in Sweden, review, 525
Fire in Florida Everglades, 4, 7
Fischler, K. J., note, 720
Fishes, deformities, in warm springs, 154
Flaccus, E., article, 692
Flanders, Stanley E., note, 165
Flooding response in a purslane, 663
Florida Everglades vegetation, 1
Florida sandhill plants, root reserve in, 292
Flour beetle, experiments on dispersal, 453
Ford, E. B., reviewed, 529
Forest associations favoring and inhibiting spruce budworm outbreaks, 608
Forest canopy light penetration, 312
Forest fires, review, 525
Forest, H. S., note, 474
Forests, upland, in Oklahoma, 593
Fosberg, F. R., note, 144, review, 754
France, vegetation of, review, 523
Francis, Roy G., reviewed, 752
Franseria acanthicarpa, 268
Fritts, H. C., article, 261
Frost action effects in Wyoming alpine tundra, 16
Fundulus confluentus, delayed hatching, 430
Furman, T., note, 140

G

Galoux, A., reviewed, 168
Galston, A. W., review, 756
Garibaldi Park, B. C., 10
Genecology, review, 519
Genetics and ecology, review, 519
Georgia granite habitats, 652
Georgia, light and pine reproduction in, 478
Germany, grasslands in, review, 171
Germination and growth following irradiation, 383
Germination in Nicotianas, 630
Germination of *Portulaca smallii,* 658
Germination, regulation of, 20
Geum turbinatum, 390, 394
Gila atraria, ecology of, 564
Goodall, D. W., review, 169
Goodwin, Melvin H., Jr. and G. J. Love, article, 198
Goreau, Thomas F., article, 67
Graham, B. F., Jr., article, 677
Granite outcrop ecology, 651
Grasslands in Germany, review, 171
Grass-legume mixture, 732
Grass, perennial native and Lehman lovegrass, 738
Grazing in Wisconsin prairies, 36
Grazing susceptibility number, 41
Great Basin postpluvial climates, 361
Great Salt Lake, bird life of, review, 528
Great Smoky Mountains, chestnut in, 349
Grieg-Smith, P., reviewed, 169
Griffin, D. R., reviewed, 527
Griffiths, J. F., note, 490
Groupements Vegeteaux de la France Mediterraneenne, reviewed, 523
Growth and shell formation in xanthid crabs, 113
Growth, radial, in Douglas-fir branches, 480
Growth-temperature curves for trees, 263
Gunter, Gordon and J. Y. Christmas, note, 724

H

Habitat, concept of, 725
Hairston, N. G., article, 404
Hairston, N. G., reviews, 167, 168, 520
Hall, I. V., note, 743
Hanson, H. C., reviews, 171, 331
Haramoto, Frank H., article, 244
Hardpan and roots, 272
Hardy, A. C., reviewed, 529
Harrar, J. G., review, 171
Harrington, Robert W., Jr., article, 430
Harris, H. C., article, 292
Harris, L. E., article, 644
Hatching, delayed, in *Fundulus* eggs, 430
Hawaii, biological control in, 244
Hawaii, vegetation on Mauna Loa, 144
Heaslip, Margaret B., article, 383
Heath-shrub mountain meadows, 12
Hedgpeth, J. W., reviewed, 744
Heliotropium convolvulaceum, 267
Hiesey, W. M., reviewed, 519
Hilaria jamesii, 644
Hironaka, M., article, 54
Hirth, H. F., article, 417
Holmgren, R. C., article, 668
Holt, G. A., note, 738
Hopkins, Brian, review, 754
Hovanitz, William, review, 529
Hubbs, Clark, note, 154
Hubbs, C. L., reviewed, 750
Human ecology of an atoll, review, 328
Human ecology, reviews, 328, 752
Hummocks, frost, 16
Hutchings, S. S., article, 668
Huxley, Julian, reviewed, 529
Hybrid oak distribution a clue to past climates, 361
Hypericum perforatum autecology, 54

I

Ice, effect on fishes, 465
Idaho, *Hypericum perforatum* in, 54
Ilex vomitoria in North Carolina, 148
Illinois, tree growth analysis in, 261
Illumination, and reproduction, *Simocephalus,* 514
Increment boring containers, 148
Indian Manual of Plant Ecology, reviewed, 753
India, plant ecology in, review, 753
Inger, Robert F., article, 127
Inhibitors, water-soluble, in germination, 30
Injection of dye into trees, 678
Insects, marine corixids, 723
International Plant-geographic Excursion, in Spain, review, 521
Invasions, ecology of, review, 168
Ipomoea leptophylla, roots, 266
Irradiation of tree seed, 383
Isaak, D., note, 317
Isopoda, distribution of *Cyathura,* 507
Isopoda, records of *Ligia* in Massachusetts, 507
Isotopes, radioactive, as tracers, 682
Israel, Oryzopsis pastures in, 20

J

Jackrabbit, carcasses on highways, 718
Jackson, L. W. R., note, 478
Jamaica, ecology of coral reefs, 67
Jensen, Paul, article, 447
John, Kenneth R., article, 564
Johnsen, T. N., Jr., note, 324, 487
Jones, Albert C., article, 465
Juniperus virginiana, 150
Juniperus spp. seeds, 487

K

Kannowski, Paul B., note, 162
Kartographische Darstellung der Vegetation des Creux due Van-Gebeites, reviewed, 524
Keay, R. W. J., reviewed, 754
Keysort punch cards in ecology, 323
Kincaid, D. R., note, 738
Klapp, Ernst, reviewed, 171
Klopfer, Peter H., article, 90
Knudsen, Jens W., article, 113
Kochia vestita, 644
Koller, D., article, 20
Krause, H. H., note, 492
Kruckeberg, A. R., review, 519
Kucera, C. L., note, 485

L

Laird, Marshall, article, 206
Lakes, arctic, limnology of, 49
Land animals, synecology of, reviews, 166, 520
Land management, reviews, 752
Landslide revegetation in White Mts., 692
Land: the Yearbook of Agriculture, reviewed, 752
Larix laricina, 317
Lasius minutus, radioactive phosphorus in colony, 162
Latrodectus, habits and venom in Israel, 515
Leach, William, reviewed, 332
Leaf litter, deciduous, 485
Learning in young anatidae, 90
Lebensgemeinschaften der Landtiere, reviewed, 520
Lehmann lovegrass spread in Arizona, 738
Levi, H. W., review, 529
Light and seedling growth, 664
Light intensity measurement, 313
Light in tobacco germination, 632
Light passage through forest canopy, 312
Light sensitivity in germination of Oryzopsis, 25
Light, visible, effect on growth of *Tetrahymena,* 512
Ligia oceanica, records at Cape Ann, Mass., 507
Limnology of arctic lakes, 49
Lindroth, C. H., reviewed, 749
Listening in the Dark, reviewed, 527
Litter, weathering of, 485
Living Resources of the Sea, reviewed, 748
Lizard, population shift, 157
Lizards, temperature responses and ecological relations of Bornean, 127
Loggerhead turtle, mortality of eggs, 303
Longevity of Hypericum seeds, 57
Longevity of Juniperus seeds, 487
Loop frequency method for cover, 668
Los Angeles, air pollution effects, 621
Love, Askell, reviews, 525, 755
Love, G. J. and M. H. Goodwin, Jr., article, 198
Loveless, C. M., article, 1
Lowry, W. P., note, 492
Lüdi Festschritt, review, 328
Lüdi, W., reviewed, 521
Lupinus, group *Micranthi,* 6
Lygosoma, population shift in eastern Missouri, 157

M

MacArthur, R. H., review, 326
Maguire, Bassett, Jr., notes, 312, 506
Major, J., comment on, 153
Major, Jack, reviews, 328, 330, 524
Mammals, and field succession in New Jersey, 249
Mammals of fence rows, 140
Mammals, small, in old field succession, 417
Mangrove, Papua, 708
Mapping of vegetation, reviews, 524, 753
Marine bacteria, in Gulf and Atlantic waters, 711
Marine bottom samples, and screen size, 307
Marine ecology, reviews, 167, 743, 745, 747, 748
Marine insects, 723
Mariscus jamaicensis, 2, 3
Maritime live oak forest, 148
Marshall, Nelson, note, 298
Marshall, W. H., note, 317
Massachusetts, Cape Cod palynology, 735
Mathematical notation in ecology, 492
Maturo, Frank J. S., Jr., article, 116
Mauna Loa, Hawaii, 144
McAlister, W. Bruce, note, 305
McClary, Andrew, note, 158
McClung, A. C., note, 315
McCormick, Jack, review, 332
McHugh, J. L., review, 749
McIntosh, R. P., note, 482
McMillan, C., note, 490
Mediterranean vegetation, review, 523
Mesquite and Lehmann lovegrass, 738
Methods in chemical oceanography, review, 746
Mice, eosinophil responses to behavioral disturbance, 156
Microbial populations in filters, 276
Microbracon, distribution of eggs, 302
Microenvironmental study of alpine snowbank habitat, 388
Micro-nutrients, 316
Midge larvae, computation of production, 425
Miller, R. S., review, 327
Minnesota bog succession (reverse), 317

Misra, R., reviewed, 753
Mites, ecology of forest floor, 557; biologies of 2 species, 572; effects of gamma rays on, 572
Mites, natural history of, review, 167
Mooney, H. A., article, 16
Moore, C. W. E., notes, 141, 735, article, 337
Moore, H. B., reviewed, 167
Moore, Walter G., article, 398
Moor, Max, reviewed, 524
Moray eels, food selection, 296
Morris, R. F., article, 580
Mosquito, populations of California foothill stream, 186
Mosquitoes, parasites of Singapore, 206
Mt. Marcy, transect above timberline, 320
Myers, Charles W., note, 157

N

National parks, Canada, 608
Naylor, Alfred F., article, 453
Needham, Paul R. and Albert C. Jones, article, 465
Neess, John and Richard C. Dugdale, article, 425
Negbi, M., article, 20
Nègre, R., reviewed, 523
Nevada, 626
New Guinea, rain forest ants, 437
New Hampshire landslides, 692
New Hampshire, root grafting, occurrence in, 677
New Jersey pine barrens, 484
New Mexico sand dune plants, roots of, 265
New South Wales tablelands soils, 337
New York, Adirondacks of, 320
New York, Shushan, white spruce outlier, 333
New York, Ulster Co., 482
Neyman distribution, 732
Niantic River, oyster sets, 298
Niche, concept of, 725
Nicotiana attenuata, 626
Nicotiana trigonopylla, 626
Nielsen, Erik Tetens and Hedvig Tetens Nielsen, article, 181
Nielsen, Hedvig Tetens, article, 181
Nitrogen in roots of sandhill plants, 292
North Atlantic biogeography, review, 749
North Carolina live oak forest, 148
Nutrients in soils of New South Wales, 337
Nuttonson, M. Y., reviewed, 754
Nypa fruticans, Papua, 709

O

Oak distribution, a clue to postpluvial climates, 361
Oak hybrid in Utah, 362
Oak-pitch pine stands in New York, 482
Oak woods, soil zoology of, review, 168
Oberdorfer, Erich, reviewed, 521
Oceanography and Marine Biology, reviewed, 747
Oceanography, reviews, 167, 744-748
Odum, E. P., review, 166
Odum, H. T., reviews, 167, 328, 745
Oemida gahani, temperature tolerance, 490
Ogilvie, R. T., note, 140
Ohio, aquatic photosynthesis, 377
Oklahoma, original forests of, 595
Oklahoma prairie algae, 474
Oklahoma prairie, phytosociological analysis of, 255
Oklahoma, upland forests of, 593
Oldfield blueberry stand populations, 742
Oosting, H. J., note, 148
Opuntia arborescens, 270
Opuntia sp. epiphytic on saguara, 324
Orange-peel bucket, modified for bottom sampling, 502
Oregon, coastal sand dunes in, review, 332
Organic layers in Alaska soils, 494
Orientation, acoustic, review, 527
Origine Photochimique de la Vie, reviewed, 755
Origin of life, review, 755
Oryzopsis hymenoides, 270, 645
Oryzopsis miliacea germination, 20
Oxygen anomalies, in Oregon surf, 305
Oyster, set on cultch, 298

P

Paleobotany in tundra, 146
Palmann, Hans, reviewed, 330
Panicum hemitomon, 4
Panicum virgatum, 255
Papuan swamps, 703
Parasites of Singapore mosquitoes, 206
Parasitism in spruce-budworm, 618
Parker, Richard A., note, 514
Parrot fishes, role of mucous envelope, 296
Patten, Bernard C., article, 221
Pearson, Paul G., article, 249
Peat in frost-cycle terrain, 17
Peat, pollen record in, 737
Penfound, Wm. T., article, 593
Penn, George Henry, note, 514
Permanent transect on a mountain summit, New York, 320
Persea borbonia, 150
Perspectives in Marine Biology, reviewed, 745
Pflanzensoziologische und Bodenkundliche Untersuchungen im Schweizerischen Nationalpark, reviewed, 330
Pflanzenwelt Spaniens, reviewed, 521
Phelps, Austin, note, 512
Phenology and water stress, 636
Phenology in the spruce budworm ecosystem, 616
Phenology of alpine plants, 394-6
Phenology, review, 755
Photochemical origin of life, review, 755
Photoperiodism in a purslane, 663
Photosynthesis in aquatic communities, 377
Photosynthesis in conifers, 63, 738
Phytoplankton photosynthesis, 377
Picea engelmanni, 611
Picea excelsa photosynthesis, 63, 738
Picea glauca in Alaska, 492; in New York, 333
Picea pungens photosynthesis, 63
Piedmont granite outcrop plants, 651
Piedmont succession, in old fields, 249
Pierre, Franklin, reviewed, 751
Pimentel, David and Paul C. White, Jr., articles, 533, 541
Pine barrens, New Jersey, 484
Pinus echinata seedlings and light, 478
Pinus rigida in New York, 482
Pinus silvestris, light penetration of canopy, 312
Pinus strobus, 677
Pinus taeda seedlings and light, 478
Pisaster, food of, 720
Plant diseases, review, 171
Plant ecology, reviewed, 332
Plant geography and ecology, 153
Plant succession, reverse, 317
Platt, R. B., article, 651
Plot size in loop frequency method, 669
Poisson distribution, 732

Poland, grass-legume-weed density statistics, 732
Poland, light passage through forests in, 312
Pollen work in Barnstable Marsh, Cape Cod, 735
Polygon-hummock cycle in alpine tundra, 16
Population Ahead, reviewed, 752
Population dynamics, reviews, 325, 326
Population dynamics, single factor analysis in, 580
Population ecology of land animals, reviews, 166, 520
Populations in blueberry stands, 742
Population studies, review, 325
Portulaca smallii, ecological life history, 651
Potter, L. D., note, 148
Prairies, grazing of, in Wisconsin, 36
Prairies, wet, in Everglades, 3
Precipitation, and black-tailed jack rabbits in Kansas, 194
Précsényi, S., note, 732
Principles of Field Biology and Ecology, reviewed, 327
Principles of Plant Pathology, reviewed, 171
Pringle, W. L., article, 54
Procecidochares utilis, used to control pamakani, 244
Productivity in snowbank environment, Medicine Bow Mts., 388
Prosopis juliflora, 738
Pseudococcomyxa adhaerens in lab solutions, 732
Pseudotsuga, missing annual layers in, 480
Puerto Rico, environments of *Australorbis* in, 533, 541
Punch card recording of field data, 323
Puri, G. S., reviewed, 753
Purslane, 651
Pyrausta nubilalis, mortality factors, 310

Q

Quantitative Plant Ecology, reviewed, 169
Quarter, point-centered, method, 694
Queen, John, note, 305
Quercus alba, growth, 261
Quercus alba leaf litter, 485
Quercus gambellii x *turbinella*, 362
Quercus incana root carbohydrates and N_2, 292
Quercus laevis food storage, 292
Quercus marilandica leaf litter, 485
Quercus prinus in New York, 482
Quercus rubra leaf litter, 485
Quercus virginiana in North Carolina, 148

R

Radioactive tracers, 681
Radioactivity, phosphorus in colony distribution of ant *Lasius minutus*, 162
Ragotzkie, Robert A., note, 303
Rainfall, affecting mortality of turtle eggs, 303
Range limit of *Picea glauca*, 333
Ray, R. J., article, 255
Recording associations on punch cards, 323
Regression analysis on tree growth, 262
Reish, Donald J., notes, 307, 502
Release of trees by death of chestnut, 356
Reukema, D. L., note, 482
Revegetation of landslides, 692
Rhode Island, pond thermocline, 152
Rhynchospora spp., 3, 4
Rice, E. L., article, 593
Rieger, S., note, 492
Rodents, effects of fire on small, 102
Rohde, Charles J., article, 572
Root grafting in eastern white pine, 677
Root systems of dune species, 265
Roppel, Alton Y. and Charles R. Weaver, note, 158
Roussine, N., reviewed, 523
Rudolph, E. D., review, 171
Rye-climate Relationships and Phenology, reviewed, 755

S

Sahara Desert, insects of, review, 751
Salisbury, E. J., review, 332
Salmon, behavior of chinook and silver, 108
Salmon, device for separating unequal sized fry, 158
Salsola pestifer, 267
Salt-desert plants, chemical content, 644
Salt-water swamps, tropical, 708
Sand dune plants, root systems of, 265
Sand dunes, coastal, review, 332
Sand dunes, insect ecology of, review, 751
Sauer, E. G. F., reviews, 526, 527
Schistosoma mansoni, 533, 541
Schwartz, Urs, reviewed, 524
Scorpions, natural history of, review, 167
Scott, J. P., reviewed, 526
Screen size, in washing marine bottom samples, 307
Sears, P. B., review, 752
Seed irradiation, effects of, 385
Seeds, *Juniperus* spp., longevity, 487
Selective action by smog suggested, 625
Sewage disposal and its ecology, 274
Sexton, Owen J., note, 715
Shawangunk Mts., New York, 482
Shepherd, R. F., article, 608
Shock disease, 727
Shulov, A. and A. Weissman, note, 515
Siegel, H. S., note, 495
Simocephalus reproduction and illumination, 514
Skogsbrandfalt i Muddus Nationalpark, reviewed, 525
Sládečková, Alena, note, 733
Slides, revegetation of, 695
Slobodkin, L. Basil, article, 232
Slomka, J., note, 312
Slope exposure and soil types in Alaska, 492
Smith, R. H., article, 333
Smog, effect on lupines, 621
Snowbank environment and vegetation, 388
Soil algae, 474
Soil animals, physical environment of, 550
Soil development, review, 330
Soil, forest, mites of, 557
Soil nutrients in New South Wales, 337
Soils and forests in Alaska, 492
Soil zoology, reviews, 167, 168
Solanum eleagnifolium, 267
Solar radiation, effect on fishes, 465
Solomon, M. E., review, 325
Sorghastrum nutans, 255
Southwestern U. S., desert tobaccos in, 626
Southwick, Charles H., note, 156
Spain, vegetation of, review, 521
Species abundance and community organization, 404
Species, experimental studies on nature of, review, 519
Sphaeralcea parviflora, 268
Spiders, natural history of, review, 167
Spiders, Scorpions, Centipedes and Mites, reviewed, 167
Sporobolus cryptandrus, 644
Spruce budworm, two-year cycle, 608
Stakman, E. C., reviewed, 171
Stannard, L. J., Jr., review, 750
Starfish, food of *Pisaster*, 721
Starlings, sex and age structure of roosting, 136
Statistical study of density estimates, 732

Statistics in plant ecology, review, 169
Stefferud, Alfred, reviewed, 752
Stipa comata, 644
Stoddart, L. A., article, 644
Stream flow, effect on fishes, 465
Stumps, old, with living roots, 687
Succession, mammals in old field, 417
Succession, on old fields in New Jersey, 249
Succession on slides and their deposits, 692
Succession, reverse plant, 317
Sulfur deficiency in soil, 315
Surf, and oxygen anomalies in Oregon, 305
Survival in spruce budworm, 617
Swamp communities in Papua, 703
Sweden, forests and forest fires, review, 525
Switzerland, plant ecology in, reviews, 328, 330, 524
Symposium on population ecology, review, 325
Synecology of land animals, reviews, 166, 520
Synthetic plant populations used, 672
Systematics of North American Daphia, reviewed, 529

T

Tamala Borbonia, 4
Tashian, Richard E., article, 589
Taylor, B. W., article, 703
Taylor, W. P., review, 168
Teasel waters, biotas of, 506
Temperature and a purslane, 665
Temperature and ecological relations of Bornean lizards, 127
Temperature and tree radial growth, 261
Temperature changes within logs, in Kenya, 490
Temperature, effect on fishes, 465
Temperature, effects on growth and reproduction in *Craspedacusta sowerbii,* 158
Temperature in Oryzopsis germination, 25
Temperature in tobacco germination, 631
Temperature-light interaction in germination, 635
Temperatures, altithermal, 367
Tendipedidae, production, 425
Tenebrionids, ecology of, review, 751
Terrestrial arthropods, natural history of, review, 167
Tetrahymena pyriformis, growth affected by visible light, 512
Tevis, Lloyd, Jr., review, 751
Texas, 626
Thermocline, visible, 152
Thermoperiod in germination, 28
Tiemeier, Otto W., article, 194
Tiffany, L. H., reviewed, 526
Timberline in British Columbia, 10
Timberline, transect above, in New York, 320
Tischler, Wolfgang, reviewed, 166
Tisdale, E. W., article, 54
Tixier, J. S., note, 738
Tobaccos, desert, life histories, 626
Tolerance limits and soil factors, 734
Tracers in grafting studies, 681
Trachelipus rathkei, distribution, 447
Transplant quadrat method, 656
Transport, overland of aquatic organisms, 312
Treatise on Marine Ecology, reviewed, 744
Tree islands in Florida Everglades, 4
Tree seedling growth after seed irradiation, 383
Tribolium confusum, dispersal, 453
Trickling filter ecology, 273
Tropical ecology, review, 753
Tropical swamp community classification, 705
Tsuga canadensis photosynthesis, 63
Tucker, J. M., article, 361
Tundra paleobotany, 146
Turner, Frederick B., article, 175
Turtles, method of estimating age, 715
Tüxen, Reinhold, reviewed, 521

U

Uca, comparative thermal death limits, 589
Udvardy, Miklos F. D., note, 724
Udvardy, M. D. F., review, 750
Uggla, Evald, reviewed, 525
Ulmus americana leaf litter, 485
UNESCO publications, reviews, 530
Upland forests of Oklahoma, 593
Utah, 626, 644
Utah, bird life of Great Salt Lake, review, 528
Utah, oak hybrid and climate, 361

V

Vaccinium angustifolium, 742
Vaccinium myrtilloides, 742
Variable-radius method, augmented, 597
Vegetation Map of Africa South of the Tropic of Cancer, reviewed, 754
Vegetation maps, Africa and Swizerland, reviews, 524, 754
Vegetation, the concept, 488
Verduin, J., note, 322
Verduin, J., article, 377, note, 738
Vernberg, F. John and Richard E. Tashian, article, 589
Vos, A. de, review, 528

W

Walford, L. A., reviewed, 749
Wallwork, John A., article, 557
Washington, coastal sand dunes in, review, 332
Washington, fence rows in, 140
Water and root development, 272
Water relations in wild tobaccos, 636
Water supply problems in the arctic, 49
Weaver, Charles R., note, 158
Weed, range (Hypericum), 54
Wells, P. V., note, 153, article, 626
Welton, M., reviewed, 328
Werner Lüdi Festschrift, review, 328
Werner, W. E., Jr., review, 327
Wetmore, C. W., note, 323
White Mts., landslide revegetation, 693
White, Paul C., Jr., articles, 533, 541
Wiesen und Weiden, reviewed, 171
Wilde, S. A., note, 492
Willson, D. L., note, 474
Wilson, Edward O., article, 437
Winn, Howard E., note, 296
Winter chemical content of desert plants, 644
Wisconsin prairies, grazing effects, 36
Woodin, H. E., note, 320
Wood rat, density of dens, 714
Wood, R. D., note, 152
Woods, F. W., article, 292
Woods, F. W., article, 349
Workbook for Field Biology and Ecology, reviewed, 327
Wyoming alpine snowbank ecology, 388

Y

Young, S. P., reviewed, 528

Z

Zoller, H., reviewed, 328
Zoogeography, reviews, 749, 750